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LOPHODERMIUM ON PINES

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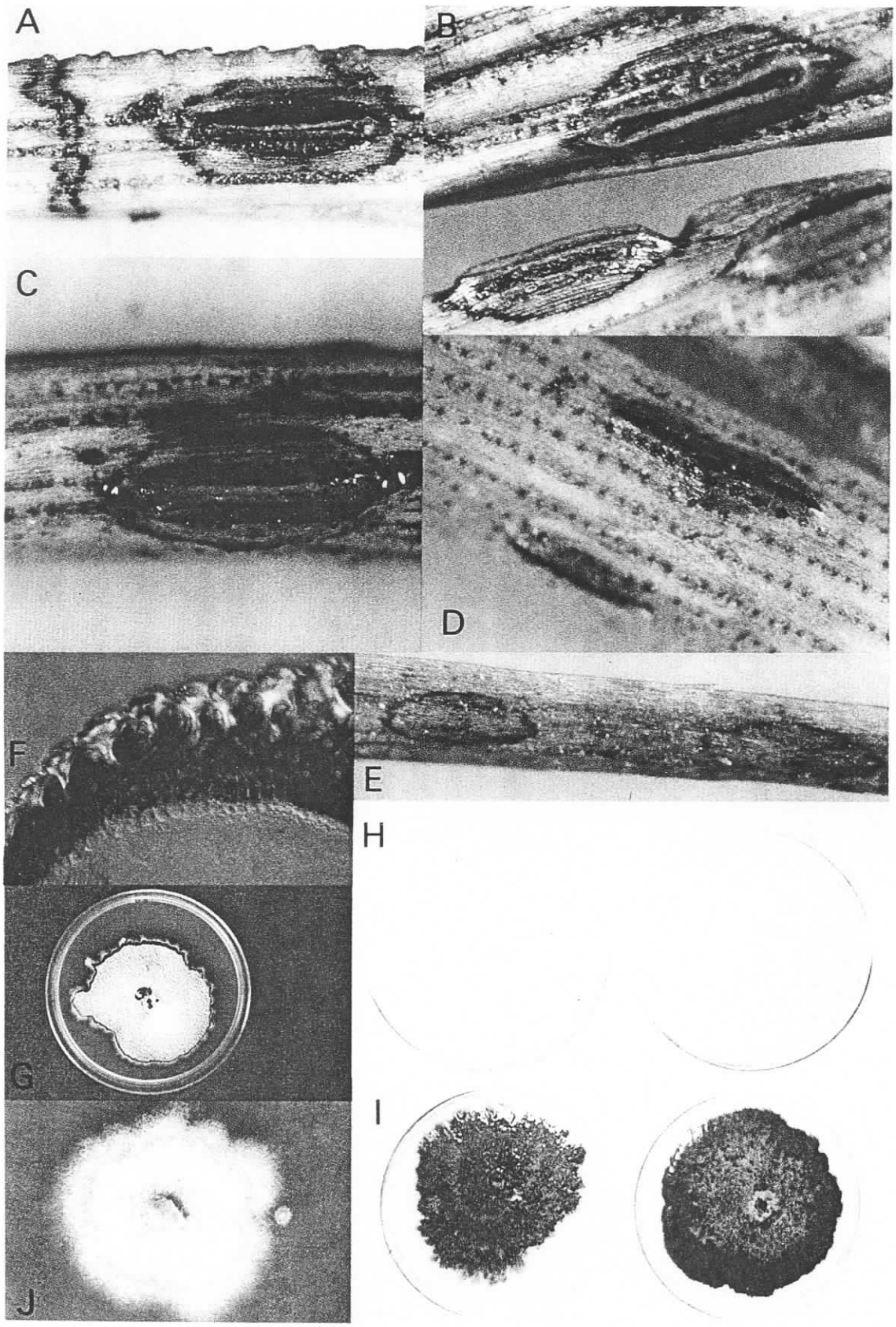

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Species of the ascomycete *Lophodermium* Chev. occurring on pines are monographed. Characteristics of their ascocarps, conidiomata, zone lines, cultures and ecology are examined in detail. Sixteen species, including *Lophodermium staleyi*, *L. indianum*, *L. ravenelii* and *L. orientale* spp. nov., together with their *Leptostroma* Fr. ex Fr. anamorphs, including *Leptostroma pinorum* var. *graupianum* var. nov., and two fungi (*Cladosporium lophodermii* and *Pseudostypella translucens*) parasitizing ascocarps of *Lophodermium* are illustrated, described and annotated. Dichotomous and synoptic keys are provided for identification and a list of twelve doubtful or excluded species, including *Sirothyriella pinastri* (Desm.) comb. nov. is appended. A bibliography of the species monographed is provided.

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INTRODUCTION

Fruitbodies of the ascomycete *Lophodermium* Chev. on needles of pine are a familiar sight to forest pathologists in many parts of the world. These fruitbodies are usually identified as *Lophodermium pinastri* (Schrad. ex Hook.) Chev., a species described originally from northern Europe, and it is generally supposed that this species is very variable in morphology and ecology but occurs wherever pines are grown. The basis for these suppositions is the large, confused and contradictory body of research literature on *L. pinastri* which has accumulated from many different countries. Most of this literature treats *L. pinastri* as the causal organism of a dangerous needlecast disease of pines, while the remainder, equally emphatically, reports it as a harmless saprophyte. Recently, however, these suppositions have been questioned, and some of the contradictions have been resolved.

Research has shown that at least four species of *Lophodermium* occur on needles of pines in Europe, and that they differ markedly in morphology and ecology. *Lophodermium pinastri* itself, one of the four species, was found to be far less variable than had previously been thought (Minter et al., 1978; Minter & Millar, 1980a, 1980b). It seems likely that previous researchers often attributed variability to *L. pinastri* simply because they failed to recognise these other species. Similarly, examination of *Lophodermium* specimens collected outside Europe reveals that most differ so much in morphology from european collections that they cannot be regarded as conspecific. This indicates that *L. pinastri* is not so widespread as was previously thought, and that reports of *L. pinastri* from outside Europe are likely often to be based on misidentifications of these other species.

Not all of these other species are totally new. Careful examination of the literature reveals that from time to time various species of *Lophodermium* have been described on pines throughout the world, and that these species have been ignored largely because their descriptions are scattered, often in obscure journals, or when available are frequently insufficient to identify the fungus. A modern taxonomic treatment of these species is clearly necessary before needlecast disease can be properly understood.

The present work attempts to supply such a treatment. The main characteristics for separating these *Lophodermium* species are reviewed. Keys are provided for identification of all species recognised, and they are described, annotated and illustrated. Fungi known to parasitize *Lophodermium* are also described, annotated and illustrated. Where possible, type material has been examined, but the work is also based on many hundreds of other specimens examined over the past six years. A bibliography of these fungi is provided after the descriptions and notes. Of necessity the work is patchy. Information about cultures, ecology and other important aspects is lacking for many species. Virtually nothing is known about their development. Collections are unrepre-

sentative, so that for example our knowledge of *Lophodermium* on secondary needles (the normal needles of a mature tree) is adequate, but almost nothing is known about *Lophodermium* on primary (seedling) needles or on cones. Doubtless therefore more species of *Lophodermium* remain to be discovered on pines. Meanwhile the treatment presented here has the obvious interim advantage of enabling the user to provide at least some sort of name to, in my experience, over 70% of specimens of *Lophodermium* on pines.

Characteristics: Apart from their ascocarps most species of *Lophodermium* also produce *Leptostroma* Fr. ex Fr. stage conidiomata, and about half produce zone lines through the substrate. Although many features can be seen by eye, or with a hand lens, the ascocarps, conidiomata and zone lines are best observed using a dissecting microscope at a magnification of between ×10 and ×50. The morphological characteristics which they display provide sufficient information to identify all species treated here. Additional useful information may be gained by examining cultures and ecology of each species, and as knowledge of these fungi increases, these two features may become more important for identification.

Ascocarps: Immature ascocarps develop totally embedded in the substrate, and appear as blackish spots on the needle or cone. This appearance is due to a black covering layer, called a clypeus, which develops between the hymenium and the substrate tissue covering the ascocarp. At maturity, the clypeus and substrate above split to reveal the hymenium. Once splitting has occurred, the degree to which the ascocarps open is determined largely by humidity. Ascocarps open when wet and shut when dry. Slide preparations of the hymenium are most easily obtained from wet ascocarps. Examination of the ascocarp external appearance and the cutting of thin sections is best carried out on dry ascocarps. Sections are necessary to determine the depth to which the ascocarp is embedded in the substrate and the structure of the clypeus and other tissues.

The depth of embedding of the ascocarp is characteristic for each species, and is best determined by examining mid-point vertical sections. Sections hand cut with a new razor are often adequate. Ascocarps of all the species, when viewed in such sections, display in order, from the outside inwards, the following features: the substrate tissue under which the ascocarp is embedded (the pine cuticle, sometimes also the epidermis and hypodermis), the clypeus (the zone of the split may be lined with colourless or pigmented lip cells), the hymenium, the sub-hymenial tissue below which there is sometimes a pigmented lower wall, and the remaining pine tissue.

Ascocarps embedded below the cuticle, but above all the other pine tissue, are described as subcuticular. In species with subcuticular ascocarps (Figs. 1, 2) the epidermal cells are separated from the cuticle, and lie in a row next to the lower wall. Species with more deeply embedded ascocarps are shown in Figs. 3, 5, 6, 8, 9 and 12. Their asco-

carps are embedded under the cuticle alone only in the central region, and the epidermal cells displaced from this region can be seen next to the lower wall. On either side of this central region, the epidermal cells have not been separated from the cuticle, and they can be seen above the clypeus. These epidermal cells are separated from the hypodermal cells which can be seen next to the lower wall. Ascocarps of this type are described as partly subepidermal. In the ascocarp shown in Fig. 7, the epidermal cells have been displaced from the central region, just as in partly subepidermal ascocarps, but on either side the cuticle, epidermis and hypodermis have remained together above the clypeus, and the lower wall is directly adjacent to the degraded mesophyll cells of the needle. Such ascocarps are partly subhypodermal. In some species none of the pine epidermal cells are separated from the cuticle (Figs 4, 10, 11, 13, 14, 15), and only hypodermal cells can be seen next to the lower wall. These ascocarps are totally subepidermal. In one species (Fig. 16, plate 1f) the clypeus arises beneath all the epidermal cells, just as in a totally subepidermal ascocarp, but in the central region a few hypodermal cells remain attached to the epidermal cells. Ascocarps of

TABLE 1 The number and position of displaced epidermal cells in ascocarps of two species of *Lophodermium* on secondary needles of various pines.

Pine species epithet	*Lophodermium pinastri*	*Lophodermium conigenum*
armandi	24 grouped	—
koraiensis	16 grouped	—
pumila	8 grouped	—
ayacahuite	11 grouped	12 grouped
densiflora	9 grouped	6 separate
leucodermis	6 grouped	—
mugo	9 grouped	5 grouped
nigra var. nigra	4 separate	5 separate
nigra var. maritima	7 grouped	6 separate
pinaster	6 grouped	5 separate
resinosa	7 grouped	—
sylvestris	8 grouped	5 separate
tabuliformis	7 grouped	5 separate
uncinata	11 grouped	—
attenuata	12 grouped	—
contorta var. contorta	9 grouped	2 separate
contorta var. latifolia	9 grouped	—
muricata	8 grouped	5 separate
virginiana	7 grouped	—
pinea	8 grouped	5 separate
palustris	8 grouped	—
durangensis	8 grouped	—
montezumae	6 grouped	—
greggii	9 grouped	—
radiata	11 grouped	—
rigida	9 grouped	—
taeda	12 grouped	—
jeffreyi	—	6 separate

this species are described as centrally subhypodermal. These differences are summarised diagramatically in Fig. 64.

The number of epidermal cells displaced, and their position by the lower wall is variable. In some ascocarps the displaced cells may be clustered in a group directly below the cuticle from which they were separated (Figs. 3, 5, 6, 12). In others they may be scattered at various points along the lower wall (Figs. 7, 8, 9). In estimating the number of cells displaced, it is important to count the indentations in the cuticle (Fig. 37 arrows) and then to try to match this figure with the number of cells visible below the ascocarp. The two figures should be reasonably close if not identical. Table 1 shows the number and position of displaced epidermal cells for two species examined on secondary needles of a wide range of pine species. Ascocarps of *L. pinastri* almost always have more than five epidermal cells displaced and grouped, regardless of the pine species, whereas ascocarps of *L. conigenum* (Brunaud) Hilitz. almost always have less than seven epidermal cells displaced and scattered. For a given species, therefore, on secondary needles, these two characteristics are probably consistent.

When partly subepidermal or partly subhypodermal ascocarps are examined in vertical sections taken from points along the ascocarp other than the mid-point, some variation in depth of embedding may be seen. Sections taken from near the extremities of these ascocarps show all the epidermal cells above the clypeus. Between these extremities and the mid-point is a region where epidermal cells are separated from the cuticle and are below the clypeus, but above the lower wall, usually in the hymenium. Serial sections of this region show such epidermal cells to be transitional between the 'up' and the 'down' position. Examples of these positions of epidermal and hypodermal cells in relation to ascocarps have been illustrated diagramatically by Minter et al. (1978). Ascocarps embedded other than in these positions are not known in *Lophodermium* species in pine.

The different positions of the epidermal and hypodermal cells have a direct affect on the external appearance of dry ascocarps (wet ascocarps of all species tend to have a uniformly black exterior, and so do not show this feature well). Where the black clypeus is covered only by the cuticle, the ascocarp surface is black. Where it is covered by both cuticle and epidermis it appears dark grey, and where it is covered by cuticle, epidermis and hypodermis it appears pale grey or brown, the same colour as the surrounding tissue. Ascocarps of subcuticular species therefore appear black over the whole extent of their clypeus. Partly subepidermal ascocarps are black in the centre and dark grey around. The proportion of black to grey is related to the number of epidermal cells displaced. Partly subhypodermal ascocarps are black in the centre and pale grey or concolorous with the substrate around this centre. Totally subepidermal ascocarps are a continuous dark grey, while centrally subhypodermal ascocarps have a pale grey or brown centre surrounded

by dark grey. These effects can be seen by comparing Figs 1-16 with Figs. 17-32, and in diagram form Figs. 63 and 64.

Although most clearly seen on mature ascocarps, the different positions of the epidermal and hypodermal cells also affect the appearance of immature ascocarps. In ascocarps of *Lophodermium* the first part of the clypeus to develop is the region around the future split. In subcuticular, partly subepidermal and partly subhypodermal ascocarps the clypeus is embedded beneath the cuticle alone in this region. Immature ascocarps of these types therefore appear as black regions with no grey surround at this stage in development. It is thus often difficult to distinguish subcuticular ascocarps from those which are partly subepidermal or partly subhypodermal when immature. Immature subcuticular ascocarps are generally somewhat circular, immature partly subepidermal ascocarps are somewhat elliptical if many epidermal cells are displaced, or long and thin if few are displaced. Immature partly subhypodermal ascocarps are similar to the partly subepidermal. Immature totally subepidermal and centrally subhypodermal ascocarps have no black area, but appear grey, gradually becoming dark grey.

The depth of embedding is also one of the factors which affects the amount to which ascocarps project above the surrounding tissue surface. In general, subcuticular ascocarps project more than partly subepidermal ascocarps, which in turn project more than the partly subhypodermal, totally subepidermal and centrally subhypodermal. Projection is however also affected by other factors. For example, wet and open ascocarps tend to project more than those which are dry and shut.

Other factors apart from depth of embedding and humidity can affect the external appearances of ascocarps. In species which have a blackened lower wall, the edge of the dry ascocarps is marked by a thin black or brownish line which occurs where this lower wall reaches the exterior of the substrate. This line is clearly seen in ascocarps which are totally grey or with a greyish surround against which it can contrast (Figs. 18, 21, 22, 23, 24, 27, 28, 29, 32). It is harder or impossible to observe in ascocarps which are totally dark grey or black (Figs. 17, 19, 20, 26). Ascocarps without a blackened lower wall do not show this feature (Figs. 25, 30, 31).

On secondary needles it is important to observe the position of ascocarps in relation to the stomata. Stomata occur in regularly spaced rows arranged longitudinally on the needle surface and cylindrical epidermal cells occupy the spaces between these rows. In most pine species rows of stomata can be seen on the abaxial and adaxial or radial sides of the needles. In the others the stomata are restricted to the adaxial or radial sides, and the abaxial surface is composed entirely of epidermal cells. In one species of *Lophodermium* ascocarps are so positioned that the zone of splitting occurs along a row of stomata (Fig. 63 *L. baculiferum*). In all the other species ascocarps are located either on a side of the needle with no stomata, or, if stomata are present, with the zone of splitting occurring between two rows of stomata (e.g. Fig. 22).

Observation of many specimens has shown that on secondary needles each species consistently shows one of the two features. The species with ascocarps splitting along a line of stomata has not been seen on primary needles. Cones have no stomata and so ascocarps on cones cannot show these features. All three species known to occur on cones also occur on secondary needles, and on secondary needles these three species all produce ascocarps splitting between two rows of stomata.

The zone of splitting itself provides a number of characteristics. On primary and secondary needles ascocarps of all species regularly open with a single longitudinal split. On cones ascocarps generally open with a single longitudinal split as on needles, but ascocarps with more than one split arranged radially are not rare (Fig. 33). This variation appears to be determined totally by the substrate. It was noted above that when examined in vertical section the clypeus may be lined with colourless or pigmented cells in the zone of the split. This lining is visible in mature ascocarps under the dissecting microscope, and is called the lips from a fanciful resemblance. Ascocarps with grey, red, orange, yellow, brown, green or blue lips have all been observed, grey being the most common. Ascocarps of some species have only grey lips. Those of other species may have lips of different colours, though for a given species usually one colour is predominant. Lip colours vary with humidity, and if sufficiently wet can be washed out entirely. This perhaps explains why grey is the commonest colour. In some ascocarps no lips are seen. The reason may be that the ascocarps are old and the lips have been lost, for example eaten by mites. Ascocarps of some species however never produce lips, and the black clypeus can be seen along the edge of the split even in recently matured ascocarps.

The size of the mature ascocarp, as seen under the dissecting microscope, is characteristic for each species. Fig. 34 shows the various dimensions which may be measured. If enough ascocarps of a species are measured on secondary needles of a given pine, the resulting histogram approaches a normal distribution in shape. This is illustrated in Fig. 35 by histograms of the perimeter line lengths of ascocarps of *L. conigenum*, *L. pinastri* and *L. seditiosum* Minter, Staley & Millar on *Pinus sylvestris* L. Pine species differ greatly in needle length, and it has been suggested that larger ascocarps are found on pines with longer needles. The mean perimeter line lengths of ascocarps of *L. pinastri* on needles of various species of pine are shown in Fig. 36. Ascocarp size is clearly unrelated to needle length in this species, or in my experience in any other. Ascocarps on primary needles and cones however tend to be smaller than those of the same species on secondary needles.

The shape of the mature ascocarp, as seen under the dissecting microscope, is similarly characteristic for each species. Much of this is determined, as noted earlier, by the extent of the clypeus and the depth to which it is embedded, but the outline of the perimeter line also varies. In some species the ascocarps are more or less elliptical, while in others they are distinctly pointed at each end (compare Figs. 17 and 23). Asco-

carps on cones tend to be less pointed than those of the same species on primary or secondary needles.

When the clypeus is examined in mid-point verticle section, it is often markedly thicker in the central region than at the sides (e.g. Fig. 16). In species with lips, the primordia of the lip cells can be seen in sections as a pale area in the centre of the clypeus even before the ascocarp has split open (e.g. Fig. 8). Lip cells appear to function as an opening mechanism. Ascocarps without lips have no such primordia (e.g. Fig. 2) and the clypeus appears to lack a mechanism, opening instead by the simple tearing of the black tissue. Examination in section of ascocarps just prior to opening is often the best way of determining for certain whether lips are present.

Thin sections of the clypeus show that the black tissue is composed of fungal cells with heavily pigmented walls. In the clypeus pigmentation is heaviest near the top and towards the centre, becoming less marked lower down and to the sides (e.g. Fig. 7). There is often a region of poorly developed pigmentation on either side of the central thickening (e.g. Fig. 1) the significance of which is apparently unknown. The cells of the clypeus, when viewed in vertical section, form a textura globulosa or angularis (Fig. 37), also in some species prismatica (Fig. 38) (Korf, 1973). Some features of the clypeus cell texture cannot, however, be seen in vertical section, and sections in another plane should be examined. The most suitable plane is the 'surface slice' (Fig. 39). In this plane the clypeus can be seen to comprise two layers. The inner is composed of cells forming a textura globulosa or angularis, and forms the bulk of the clypeus. The outer, located adjacent to the tissue beneath which the clypeus is embedded, and one cell deep, is composed of lobed cells forming an irregular textura epidermoidea (Korf, 1973) (Fig. 40). This layer was first observed by Tehon (1935) who described it as aliform tissue. Aliform tissue is present in the clypei of almost all species of *Lophodermium* on pines. It is also present, albeit in a less well developed state, in pigmented lower walls.

The hymenium of all species is composed of paraphyses and asci containing ascospores (Figs 41, 42). The paraphyses are threadlike, colourless, septate or aseptate, usually unbranched, and often hooked or swollen at the apex. Asci arise from near the base of paraphyses, and grow up between them. When mature, they are clavate or more or less cylindrical, with or without a stalk region in which no spores are seen, thin walled, with an apical pore negative in iodine, and are roughly the same length as the paraphyses. The asci lengthen rapidly at maturity, making it difficult to be certain whether the paraphyses extend above the ascus tips to form an epithecium. Ascospores are threadlike, colourless and aseptate, arranged in a bundle, eight per ascus, often coiled in a helix. They are immersed in a more or less obvious mucous sheath, and may coil up in a spiral following discharge from the ascus (Allitt, 1979). Characteristics of the hymenium are rarely if ever needed to separate the species of *Lophodermium* on pine. Various developmental studies have been

made on the ascocarps of pine inhabiting *Lophodermium* species (Jones, 1935; Gordon, 1966, 1968; Morgan-Jones & Hulton, 1977, 1979). Results appear to be conflicting, but much of the disagreement has been shown by Morgan-Jones & Hulton (1977) to stem from a basic misunderstanding of the development of *L. nitens* Darker by Gordon. Developmental characteristics are not used in this work to distinguish species.

Conidiomata: *Leptostroma* stage conidiomata of *Lophodermium* species are simple structures by comparison with the ascocarps. They are always embedded in the substrate, and when viewed under the dissecting microscope appear as circular to elliptical pustules which are black, brown or roughly the same colour as the surrounding tissue, sometimes surrounded wholly or partly by a dark perimeter line (Figs. 44, 46, 48). Individual conidiomata are always smaller than ascocarps, but in some species conidiomata can coalesce laterally (Fig. 49) or longitudinally (Fig. 50) forming multiple fructifications which may be larger than individual ascocarps. The conidiomata open by a longitudinal split to one side of the fructification or by several splits across the surface and/or by one to several ostioles, which may be scattered over the surface, located singly or in a small group in the middle of the surface, or singly or in neat longitudinal rows to one side of the conidioma. Ostioles are often hard to observe under the dissecting microscope, and usually can be seen only when they are located in the middle of the surface of paler conidiomata, when they appear as a small black spot (Fig. 44). Ostioles are better observed using slide preparations of surface slice sections. These differences are illustrated diagramatically in Fig. 65.

The depth to which conidiomata are embedded varies, and is best examined, as in ascocarps, using mid-point vertical sections. Sections hand cut with a new razor are often adequate. Conidiomata of all the species when viewed in such sections display in order, from the outside inwards, the following features: the substrate tissue under which the conidioma is embedded (the pine cuticle, sometimes also the epidermis), a more or less darkened upper fungal wall, always only one cell thick (this may be so poorly developed that it is only present around the ostioles or splits in some species), a layer of conidia and conidiogenous cells, sometimes also with larger cells interspersed which may have a sexual function as trichogynes (Jones, 1935), and a lower wall of hyaline to slightly pigmented cells, several cells thick, the walls of the lower of these cells sometimes being blackened. Below all this is the remaining pine tissue. Conidiomata may be subcuticular (Fig. 43) or subepidermal (Figs 45, 47). Partly subepidermal, partly subhypodermal and other depths of embedding have not been seen in *Leptostroma* anamorphs of *Lophodermium* on pine.

Seen in vertical section, the conidioma upper wall, being one cell thick, has few characteristics. It closely follows the outline of the tissue under which it is embedded, and may be markedly darker in the region of ostioles or splits. If the conidioma has split open at one side, the upper

wall may be thickened at this point to be several cells thick, and these cells in vertical section form a textura globulosa, angularis or prismatica. The wall is not thickened below splits which are located in the conidioma surface rather than to one side. More features of the conidioma upper wall are revealed by surface slice sections. In this plane most or all of the upper wall is composed of cells with more or less blackened walls forming a textura angularis. Wall blackening is more marked near ostioles and splits, and in some conidiomata also round the edge, accounting for the perimeter line. The upper wall of subcuticular conidiomata is generally more blackened than that of subepidermal conidiomata. The perimeter line of some conidiomata is formed of aliform tissue similar to that observed in ascocarps of most species. Ostioles located in the upper wall appear as circular holes in the wall (Fig. 51). In subepidermal conidiomata with ostioles in the centre of the upper wall careful examination reveals a thin split above the ostiole, between two epidermal cells or through a single epidermal cell, and in both cases also through the overlying cuticle (Fig. 52).

In verticle section, the conidioma lower wall is composed of cells with more or less blackened walls forming a textura angularis out of which the conidiogenous cells arise. Conidiogenous cells are similar in all species, differing only in size. Conidia are rod shaped (Fig. 53) or sometimes almost threadlike (Fig. 54), and are produced by the holoblastic sympodial development as can be seen by the characteristic 'rabbit's ears' when two conidia are attached to a conidiogenous cell (Figs 53 and 54 arrows). Reports of phialidic development of *Leptostroma* conidia appear to be erroneous. Larger cells which may be trichogynes are sometimes seen among the conidiogenous cells. Since they are rarely observed they are not used as a characteristic in this work. As the conidia have never been seen to germinate, it is possible that they have a sexual function as spermatia in connection with these possible trichogynes. There has been no recent research on this question.

Zone lines: Ascocarps and conidiomata of many species of *Lophodermium* are accompanied on the substrate by zone lines running through the pine tissue. The species vary considerably in their ability to produce these lines. In some the lines are common and easily observed, while in others they are infrequent and faint. Even within a single species great variation can occur, apparently often determined by humidity at the time of development, wet conditions stimulating line production (Brouard, 1979). The lines probably mark the edges of individual colonies in the substrate. Two lines very close together, marking two colonies are thus often seen. Zone lines may be brown or black. No species is known which produces both types. Sometimes different species occupy different parts of the same needle, and black and brown lines may be seen on one needle when this happens. Presumably black and brown lines could also occur on a single cone scale, though this has not yet been observed. This phenomenon may cause confusion, for example where a species not

normally producing lines appears to do so simply because it is close to an abundant line producing species.

Black lines are always thin and clearly marked off from the surrounding tissue. Brown lines are broader and diffuse, merging into the surrounding tissue. The black lines occur in more species, and are usually produced in greater abundance than the diffuse brown lines. Examples of each are shown diagramatically in Fig. 63. The differences in appearance of the two types of lines are related to their microscopic structure, which is best examined in slide preparations of sections taken diagonally through them. The black lines, which may extend right through the substrate, or on needles sometimes stop at the endodermis, are composed of lobed, pigmented, dark walled cells often similar to those of aliform tissue in the the ascocarp lower walls. The brown lines, which extend right through the substrate, appear to result from a brown pigment being layed down in the decomposing substrate tissue, and fungal cells are infrequent and may be absent.

Cultures: Cultures of *Lophodermium* may be obtained by single or multi-ascospore isolates, or by placing an excised hymenium or surface sterilised portions of the substrate bearing fructifications onto agar. Cultures recognisable as species of *Lophodermium* are also obtained frequently from portions of the substrate on which no fructifications are visible, including portions of apparently healthy green needles. Cultures isolated from conidia are not known. Of the pinocolous species, about six have been described in culture. Nobody has attempted, apparently, to isolate any of the others. Unless otherwise stated, all features of cultures discussed in this work are from isolates on 2% malt agar in 90mm petri dishes under natural light at room temperature.

Ascocarps have never been produced in agar culture. Although there are various reports of ascocarps on sterilised needles placed on cultures, they cannot yet be produced reliably by this method. Some isolates produce conidiomata in pure culture more or less abundantly. In these isolates conidiomata can also be produced by placing sterilised needles on the cultures. Conidiomata produced in vitro and in vivo have never been compared, and there are no adequate descriptions of them in vitro. The only comparisons made have been in conidia lengths. Conidia lengths of individual species in vitro and in vivo do not differ greatly.

Species which produce zone lines on the natural substrate can also produce the same type of zone line in culture. The zone lines appear in culture on the circumference of the colony when radial growth ceases. If growth in one region ceases earlier, perhaps due to the presence of a contaminant, line production begins earlier in that region. Cultures producing thin black zone lines may also produce a black crust over some or all of the colony surface. Cultures producing diffuse brown zone lines never produce a black crust, although their surface may become more or less brown, sometimes so brown that the zone line at the edge cannot be distinguished from the surface colouring.

In most younger isolates the predominant colour is white, and isolates of some species usually retain this colour when older apart from any zone lines present. Isolates of other species may, sooner or later, develop characteristic brown, tan or orange colours. These colours may be specific characteristics, and are not restricted to species producing zone lines. Isolates vary in speed and extent of radial growth. Some increase in diameter comparatively quickly ($>$ 4mm/day), others being slower. Growth may cease well before the edge of the dish is reached, or may continue over the whole agar surface. Mycelial branching patterns also vary and are best examined in young isolates. In some the branching is dense, forming a compact colony, while in others it is lax and the colony is fluffy. Isolates with lax branching tend to grow more quickly than those with dense. In some isolates with lax branching growing hyphae curve predominantly in one direction, giving young cultures a swirling or spiral appearance. This has never been observed in isolates with dense branching.

Differences in nutrient requirements and ability to alter the pH of the medium are known between isolates of *Lophodermium* from pine. It is not at present clear whether these are varietal or specific, as all the work was carried out on cultures purporting to be *L. pinastri*.

Ecology: Virtually nothing has been published about the ecology of *Lophodermium* species on primary needles or cones, and so all ecological studies discussed here concern *Lophodermium* on secondary needles. In only very few of these can the species of *Lophodermium* studied be satisfactorily identified. Thus, although much is known about the ecology of the genus on pines, little is known about individual species, and most of this comes from research in Europe and North America. The only detailed studies available concern *L. conigenum*, *L. pinastri* and *L. seditiosum* on *P. sylvestris* in Scotland (Millar & Richards, 1975; Minter, 1977; Minter & Millar, 1980a).

In Scotland these three species were readily isolated from apparently healthy green needles varying in age from less than one year old to four years old. Isolations were in small amounts, but increased as the needles grew old. In younger needles isolates of *L. conigenum* and *L. seditiosum* were most common, but *L. pinastri* became dominant as the needles aged. Depending on what happened to the needle during its life, a different species of *Lophodermium* fruited on it when it had died. Five categories of secondary needles were defined on which *Lophodermium* was known to fruit:

1. Senesced needles. Normally *P. sylvestris* retains needles for two to four years. These needles are green until their final summer, when they turn yellow, die and in the autumn fall to the litter, where *Lophodermium* may subsequently fruit.
2. Attached, prematurely killed needles. Damage to the stem or branch of a tree often results in the death of otherwise healthy needles still attached to the shoots (known as trash). Such

damage may be natural (e.g. windthrow, snow break, fire, attack by stem or root fungi, deer or rodents), or may be caused by man (e.g. brashing or felling). Since such damage is often by chance, it can happen at any time of year, though perhaps most often in winter. Thus needles of all ages from newly flushed to senescent occur in this category.

3. Removed, prematurely killed needles. Healthy needles removed prematurely from their twig (e.g. by wind or animals) fall green to the litter where they die and turn brown. Needles of all ages occur in this category since, like category 2, this is a chance event.
4. Needles killed by fungi other than *Lophodermium*. *Lophodermium* is only one of many organisms which infect needles. *Lophodermella sulcigena* (Rostr.) Höhn. for example causes premature browning of at least parts of needles. Attack by *L. sulcigena* is sometimes halted by an apparent hypersensitive response by the host. The needle portion killed is sometimes colonised by a *Lophodermium*. *Lophodermium* can therefore infect needles in a secondary capacity.
5. Needles killed by *Lophodermuim*. These have been observed in nurseries and young plantations. When needles less than one year old are attacked, damage may be severe and dramatic.

Of these five rather simplified categories, common observation shows three (1, 2 and 5) to be the largest source of substrate for *Lophodermium*. *Lophodermium pinastri* fruited on senesced needles (category 1), *L. conigenum* on attached prematurely killed needles (category 2), and *L. seditiosum* on needles which it had killed (category 5). *L. seditiosum* is also found on prematurely killed needles (category 2), but only when *L. conigenum* is absent (Minter, 1980b). It seems likely that similar striking habitat preferences remain to be found on other species of *Lophodermium* outside Europe.

In the same study in Scotland, it was found that the three species of *Lophodermium* produced conidiomata and ascocarps, and released ascospores at different times of year from each other. This has also been reported for *L. canberrianum* Stahl ex Minter & Millar and *L. pinastri* on pines of the *ponderosa* group in Australia (Stahl, 1966). The fruiting periods of other *Lophodermium* species on pine remain unknown.

Note: Where the mark '0' appears after a pine host in the following text, this indicates that the species of *Lophodermium* in question may not be native on this pine.

Where the same mark appears after a country in the following text, this indicates that the species of *Lophodermium* in question may not be indigenous in this country.

Literature: In much of the past literature on *Lophodermium* on pines it is impossible to recognise what species are under study. Nevertheless much of this literature is valuable. A selected list of the literature on *Lophodermium* on pines is presented below under suitable headings, to augment the literature lists presented after the treatment of each species.

Where the mark '⁰' appears after a reference, this indicates that the work is recommended.

Main sources: Darker (1932, 1967), Minter (1980a), Stephen & Millar (1975), Tehon (1935).

Ecology: Arsdel (1964), Costonis & Sinclair (1967, 1968, 1972), Gremmen (1957, 1960), Grzywacz (1973), Grzywacz & Wazny (1973), Kendrick & Burges (1962), Langner (1963), Lanier 1967a, 1968a, 1969), Lanier & Aussenac (1969), Lanier & Sylvestre (1971), Lanier & Zeller (1968), Lanier et al. (1969), Millar (1975), Millar & Richards (1975), Minter (1977, 1980b), Minter & Millar (1980a⁰), Mitchell & Millar (1978a, 1978b), Mitchell, Millar & Minter (1978), Murray & Young (1956), Pagony (1968, 1971), Prljincevic (1972), Rack (1955, 1959a, 1959b, 1961, 1963), Skilling & Nicholls (1975), Staley (1975a, 1975b⁰), Toole (1939), Verrall (1936), Watson (1971).

Hyperparasites: Georgescu & Tutumaru (1958), Minter (1980b), Reid & Minter (1979).

Taxonomic: Bisby (1923⁰), Darker (1932⁰, 1967⁰), Diedicke (1913), Eriksson (1970), Hilitzer (1929), Minter (1977, 1980a⁰), Minter & Jančařík (1980), Minter & Millar (1978a), Minter, Staley & Millar (1978), Staley (1975b⁰), Tehon (1935⁰), Terrier (1942⁰).

Cultures: Fries (1938), Kögl & Fries (1937), Langner (1933), Lanier (1968b), Lanier & Hubbes (1967, 1969), Millar & Richards (1975), Minter (1977), Minter & Millar (1980b⁰), Pagony (1976), Rack (1975), Robbins & Schmidt (1939), Scholz & Stephan (1974, 1975), Staley (1975b⁰), Stephan (1973a⁰, 1973b⁰, 1975⁰).

Development: Banfield (1960), Costonis & Sinclair (1968), Costonis, Sinclair & Zycha (1970), Gordon (1966, 1968), Jones (1935⁰), Likhité (1926), Morgan-Jones & Hulton (1977⁰, 1979⁰), Schütt & Lang (1975), Silverberg & Morgan-Jones (1974), Staley (1975a), Stephan (1969a⁰, 1969b⁰, 1971⁰), Uecker & Staley (1973).

Physiology: Fries (1938), Hattemer (1964), Kögl & Fries (1937), Krinitski (1974), Langner (1933), Lanier (1968b), Lanier & Hubbes (1969), Rack (1959a), Robbins & Schmidt (1939), Scholz (1973), Scholz & Stephan (1974⁰, 1975⁰), Schütt (1971a), Stephan (1973b⁰, 1975⁰), Wille (1927, 1929, 1933).

Leptostroma stage: Diedicke (1913), Jones (1935), Minter (1980a), Schütt & Lang (1975).

Control: Fungicides: Affeltranger (1972), Anon (1955, 1964, 1966), Chwalinski (1964, 1972, 1974), Costonis & Banfield (1964), Eggert (1959) Fystro (1961), Jamalainen (1956), Jančařík (1965, 1967), Jančařík & Temmlová (1965, 1968), Jancarik, Temmlová & Brejcha (1966), Jung (1960), Klingström (1974), Küthe (1959), Lanier (1970), Luthardt & Lyr (1972), Merrill & Kistler (1975, 1977), Nicholls (1973), Nicholls & Skilling (1974), Pagony (1963, 1964, 1971), Petersons (1930), Petrescu (1971), Powell & Leben (1973), Rack (1958, 1965, 1972), Reindl (1968, 1969), Rimkus (1959), Schicke (1959), Schindler (1970), Schönhar(1956, 1959), Shevchenko (1961), Skilling (1974), Skilling & Nicholls (1971,

1973, 1975), Taconis & Besemer (1959), Usčuplić (1964, 1976), Vedernikov (1966), Vladislav (1963), Vsevolozhskaya (1959), Witcher et al. (1975), Yakovlev (1967), Yakovlev & Molotkova (1975), Ziller (1972).

Timing: Anon. (1955), Behrndt (1963), Brennejzen (1958), Costonis & Banfield (1964), Dufrénoy (1926), Engelbrecht (1928), Fystro (1961), Hanso (1963), Jamalainen (1956), Jančařík & Temmlová (1968), Jung (1960), Klingström (1974), Mandel (1950), Merrill & Kistler (1977), Minter & Millar (1980a), Nicholls (1973), Nicholls & Skilling (1972), Pagony (1963, 1964, 1970, 1971), Peace (1953), Petersons (1930), Powell & Leben (1973), Rack (1955), Rimkus (1959), Schicke (1959), Schindler (1970), Shevchenko (1961), Usčuplić (1976), Yakovlev (1967).

Resistance: Physiology: Hattemer (1964), Iyer et al. (1971a, 1971b, 1972), Krinitski (1974), Pagony & Prem (1969), Scholz (1973), Scholz & Stephan (1974, 1975), Schuck (1969, 1972), Schütt (1971b), Wille (1927, 1929, 1933).

Trials and Breeding: Björkman (1971, 1972, 1973), Bolland (1957), Bolsinger (1958), Dengler (1955a, 1955b), Eckstein (1973), Schütt (1957, 1958, 1959, 1964a, 1964b, 1965).

Sporulation periods: Chiba & Zinno (1967), Chwalinski (1964, 1971), Costonis & Sinclair (1972), Engelbrecht (1928), Hanso (1963, 1968), Kozlowska (1968), Lanier (1968a), Lanier & Sylvestre (1971), Lebkova (1967), Linzon (1968), Luthardt (1968, 1971), Manka (1956), Millar (1975), Minter (1977), Minter & Millar (1980a[0]), Nicholls & Skilling (1974), Pagony (1964, 1968), Peace (1953), Powell & Leben (1973), Rack (1963, 1965), Rimkus (1959), Schütt (1960), Shevchenko (1960), Usčuplić (1976), Vedernikov (1964), Yakovlev (1967).

Keys to species of *Lophodermium* on *Pinus*: 1 Dichotomous

1.	On needles	2
	On cones	20
2. (1)	On primary needles (seedlings 1, 2, and 3 years old) ...	3
	On secondary needles (plants more than 1 year old) ...	4
3 (2)	Ascocarps associated with thin black zone lines across the needle ... ... *L. pinastri* (p. 23)	
	Ascocarps not associated with thin black zone lines across the needle... ... *L. seditiosum* (p. 34)	
4. (2)	Ascocarps centrally subhypodermal ... . *L. durilabrum* (p. 41)	
	Ascocarps otherwise embedded	5
5. (4)	Ascocarps totally subepidermal	6
	Ascocarps otherwise embedded	11
6. (5)	Ascocarps splitting open along a line of stomata ... ... *L. baculiferum* (p. 21)	
	Ascocarps splitting open along a line of epidermal cells	7
7. (6)	Ascocarps with lips	8
	Ascocarps without lips	10

8. (7)	Conidia of *Leptostroma* stage more than 15μm long	*L. ravenelii* (p. 33)	
	Leptostroma stage absent or conidia less than 15μm long	9	
9. (8)	Ascocarps with pigmented basal wall	*L. seditiosum* (p. 34)	
	Ascocarps without pigmented basal wall	*L. canberrianum* (p. 40)	
10. (7)	Thin black zone lines present ...	*L. pini-pumilae* (p. 38)	
	Thin black zone lines absent ...	*L. orientale* (p. 40)	
11. (5)	*Leptostroma* stage subcuticular	12	
	Leptostroma stage subepidermal or absent	14	
12. (11)	Ascocarps with lips	*L. molitoris* (p. 20)	
	Ascocarps without lips	13	
13. (12)	Ascocarps totally black in external appearance	*L. nitens* (p. 17)	
	Ascocarps black in the centre, with a grey surround	*L. sp.*[1] (p. 19)	
14. (11)	Ascocarps partly subepidermal	15	
	Ascocarps partly subhypodermal	19	
15. (14)	Ascocarps without pigmented basal wall	*L. australe* (p. 32)	
	Ascocarps with pigmented basal wall	16	
16. (15)	Ascocarps associated with many thin black zone lines across the needle...	*L. pinastri* (p. 23)	
	Ascocarps not associated with thin black zone lines across the needle...	17	
17. (16)	Mean ascocarp perimeter line length greater than 1000μm	*L. conigenum* (p. 28)	
	Mean ascocarp perimeter line length less than 1000μm	18	
18. (17)	Conidia of *Leptostroma* stage more than 8μm long	*L. staleyi* (p. 22)	
	Conidia of *Leptostroma* stage less than 9μm long	*L. pini-excelsae* (p. 37)	
19. (14)	Ascocarps without pigmented basal wall	*L. australe* (p. 32)	
	Ascocarps with pigmented basal wall	*L. indianum* (p. 27)	
20. (1)	Mean ascus length less than 130μm, lips of ascocarp often red	*L. pinastri* (p. 23)	
	Mean ascus length greater than 130μm, lips of ascocarp other colours	21	
21. (20)	Mean ascus length less than 170μm, lips of ascocarp often blue	*L. seditiosum* (p. 34)	
	Mean ascus length greater than 170μm, lips of ascocarp often green ...	*L. conigenum* (p. 28)	

Keys to species of *Lophodermium* on *Pinus*: 2 Synoptic, for specimens on secondary needles only

Ascocarp features	
Subcuticular	1, 2, 3, 6 sometimes on five-needle pines
Partly subepidermal	3, 5, 6, 8, 9, 12
Partly subhypodermal	7, 9
Totally subepidermal	4, 10, 11, 12, 13, 14, 15
Centrally subhypodermal	16
Pigmented basal wall present	1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12, 16
Pigmented basal wall absent	9, 13, 14, 15
Splitting open along a line of stomata	4
Splitting open along a line of epidermal cells	1, 2, 3, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16
Lips present	3, 5, 6, 7, 8, 9, 10, 11, 12, 15
Lips absent	1, 2, 4, 13, 14, 16
Lips red	6, 8 rarely when old and dry
Lips green	6 rarely when wet, 8, 11
Lips blue	11
Conidioma features	
Conidiomata present	1, 2, 3, 4, 5, 6, 8, 9, 10, 11, 12, 13
Conidiomata absent	7, 14, 15, 16
Conidiomata easily missed	12, 13
Subcuticular	1, 2, 3
Subepidermal	4, 5, 6, 8, 9, 10, 11, 12, 13
Markedly coalescing laterally	4
Markedly coalescing longitudinally	8, 11 sometimes
Opening by a longitudinal split to one side of the conidioma	4, 5, 6, 8 sometimes, 9, 10, 11 sometimes, 12, 13
Opening by central ostioles	8, 9, 10, 11, 12, 13
Conidia mean length $>9\mu$m	4, 5, 10
Zone line features	
Thin black zone lines present	1, 2, 3, 4, 5, 6, 7, 13
Diffuse brown zone lines present	8, 10, 11

1. **Lophodermium nitens** Darker, *Contributions from the Arnold Arboretum of Harvard University* **1**: 74, 1932. (Figs 1, 17, 37, 38, 43, 63, 64, 65).

≡ *Lophodermina nitens* (Darker) Tehon (1935).

Diagnostic features: Ascocarps totally black, subcuticular, without lips; conidiomata subcuticular; zone lines black, abundant; on haploxylon pines.

Ascocarps on secondary needles, predominantly on the abaxial side, shiny, black whether wet or dry, with a clearly marked outline, elliptical or

slightly pointed at each end, raising the surface of the needle, 600-850μm long (perimeter line), opening by a single longitudinal split, lips absent; in mid-point vertical section subcuticular, the clypeus often being thickened in the region of the split and extending on either side to meet the basal wall which is poorly developed, cells forming a textura prismatica being sometimes visible where the clypeus and basal walls join; in surface slice section aliform tissue is present in both the clypeus and the basal wall. *Paraphyses* tips hooked and slightly swollen. *Asci* 95-135 $\times$ 11-13μm. *Ascospores* 80-120 $\times$ 2μm.

Conidiomata on secondary needles, predominantly on abaxial side, pale brown to black and shiny, with a clearly marked outline, more or less circular, raising the needle surface, smooth or wrinkled, 50-400μm diameter, with one to several inconspicuous ostioles, also opening by one or more irregular tears in the surface; in mid-point vertical section subcuticular; in surface slice section the upper wall extends over the whole conidioma, with ostioles seen as circular pores 3-10μm diameter, occurring scattered in the upper wall, the cell walls of which may be noticeably more blackened near the ostioles or splits. *Conidiogenous cells* 8-12 $\times$ 2.5-4μm. *Conidia* rod shaped, 6-9 $\times$ 1μm. *Zone lines* black, usually abundant.

Typification: On needles of *Pinus strobus*, Timagami, Ontario, Canada, May 1924, J. H. Faull, Herb. J. H. Faull 4882, now in FH, holotype (Darker, 1932).

Selected specimens examined: On *P. strobus*, Timagami, Ontario, Canada, 27 May 1924, G. D. Darker, isotype, K; also IMI 23091, 23092, 23093, 23109, 23111, 23112, 23113, 23114, 142256, 216495, 239363.

Hosts: *Pinus albicaulis*, *P. lambertiana*, *P. monticola*, *P. strobus*.

Distribution: North America: Canada (British Columbia, Nova Scotia, Ontario), United States (California, Idaho, Maine, Massachusetts, Michigan, New Hampshire, Oregon, Pennsylvania, Washington).

Cultures: No information.

Fruiting period: No information.

Ecology: Known only from secondary needles of haploxylon pines; probably fruits saprophytically on fallen senesced needles which have overwintered in the litter.

Notes: Gordon (1966, 1968) reported that ascocarps of *L. nitens* develop differently from those of other members of the family in that the developing hymenium is composed of characteristic dark cells forming a textura prismatica. On this basis Staley (1975b) proposed that *L. nitens* and two other unnamed North American taxa should be separated into a different subgenus from other pinicolous *Lophodermium* species. The subgenus was not validly published. Morgan-Jones & Hulton (1977) have subsequently shown convincingly that Gordon's report was based on a mix-interpretation and that *L. nitens* develops no differently from any other species of *Lophodermium*.

Literature: Boyce (1940), Darker (1932, 1967), Gordon (1966, 1968), Lanier (1967b), Minter (1977, 1980a), Minter & Millar (1978a), Morgan-Jones & Hulton (1977), Staley (1975b), Tehon (1935).

2. Lophodermium sp.[1] (Figs 2, 18, 63, 64, 65)

Diagnostic features: Ascocarps black with a grey surround and a black perimeter line, subcuticular, without lips; conidiomata subcuticular; zone lines black, abundant; on haploxylon pines.

Ascocarps on secondary needles, predominantly on the abaxial side, when wet shiny and black, when dry shiny and black in the centre for about half the total surface area, with a grey surround and a black perimeter line making a clearly marked outline, round to elliptical, raising the surface of the needle, 600-1100μm long (perimeter line), opening by a single longitudinal split, lips absent; in mid-point vertical section subcuticular the clypeus becoming paler on either side and not extending as far as the basal wall which is poorly developed; in surface slice section aliform tissue is present in both the clypeus, where it is poorly developed, and the basal wall. *Paraphyses*, *asci* and *ascospores* not mature in the specimen examined. *Conidiomata* indistinguishable from those of *L. nitens*. *Zone lines* black, abundant.

Typification: None.

Specimen examined: On needles of *Pinus sibirica*, Krasnoyarskiy Krai, Krasnoyarsk, U.S.S.R., 25 Nov. 1955, A. Yavorskiy, IMI 75985a.

Hosts: *Pinus sibirica*.

Distribution: Asia: U.S.S.R. (Krasnoyarsk).

Cultures: No information.

Fruiting period: No information.

Ecology: Known only from secondary needles of haploxylon pines; possibily fruits saprophytically on fallen senesced needles which have overwintered in the litter as *L. pinastri* which is known to have this ecology is also present in the specimen.

Notes: In the only known collection of this species, the ascocarps are immature, the paraphyses not fully formed, and the asci and ascospores absent. Although *Lophodermium sp.*[1] is almost certainly new and undescribed, the absence of asci makes it impossible to publish legitimately a description of it as a new species (Article 59, Stafleu et al., 1972). It has, however, ben placed in *Lophodermium* for the following reasons: on pines only species of *Lophodermium* and *Meloderma* Darker are known to have subcuticular *Leptostroma* conidiomata as anamorphs. Of these two genera, subcuticular ascocarps and production of black zone lines are known only in *Lophodermium*.

Lophodermium sp.[1] is similar to *L. nitens*, the only other species to have subcuticular ascocarps without lips. They differ mainly in the external appearance of the ascocarps, which in *L. sp.*[1] are often nearly circular and have a grey surround within the perimeter line, compared to those of *L.*

nitens which are elliptical, often pointed, and totally black, even when immature. The grey surround in ascocarps of other species of *Lophodermium* is caused by the partly subepidermal or partly subhypodermal development. In *L. sp.*[1] this is not the case, and the grey surround occurs simply because the blackened clypeus does not extend as far as the perimeter line.

Literature: None definite. Publications treating *L. pinastri* on *P. sibirica* may refer to this species, e.g. Lebkova (1967).

3. Lophodermium molitoris Minter, *Canadian Journal of Botany* **58**: 908, 1980. (Figs 3, 19, 44, 63, 64, 65)

Diagnostic features: Ascocarps black, subcuticular or partly subepidermal, with lips; conidiomata subcuticular; zone lines black, infrequent to abundant.

Ascocarps on secondary needles, on all sides, when wet shiny and black, when dry shiny and black, or black in the centre for more than half the total surface area, with a dark grey surround with a black perimeter line making a clearly marked outline, elliptical, raising the surface of the needle, 500-1000μm long (perimeter line), opening by a single longitudinal split, lips present, grey; in mid-point vertical section subcuticular, or partly subepidermal, in which case the epidermal cells remaining above the ascocarp may nevertheless be separated from the cuticle and embedded in the clypeus which in any case is less blackened in a small zone on either side of the split, but extends on either side as far as the basal wall which is well developed, cells forming a textura prismatica being sometimes visible where the clypeus and basal wall join; in surface slice section aliform tissue is present in both the clypeus and the basal wall. *Paraphyses* tips unswollen. *Asci* 90-130 $\times$ 10-14μm. *Ascospores* 80-120 $\times$ 2μm. *Conidiomata* more elliptical, otherwise indistinguishable from those of *L. nitens*. *Zone lines* black, infrequent to abundant.

Typification: On needles of *Pinus banksiana*, Macdowall, Sask., Canada, 23 July 1935, R. C. Russell, IMI 23110, holotype.

Specimens examined: On *P. banksiana*, Macdowall, Sask., Canada, 23 July 1935, R. C. Russell, IMI 23110, holotype, also IMI 23098, 23103, 23115, 73332, 245440.

Hosts: *Pinus banksiana, P. rigida, P. virginiana.*

Distribution: North America: Canada (N.W. Territories, Ontario, Saskatchewan), United States (Georgia).

Cultures: No information.

Fruiting period: No information.

Ecology: Known only from secondary needles of diploxylon pines.

Notes: Ascocarps of *L. molitoris* vary between different collections in the depth to which they are embedded. In some collections the ascocarps contain needle epidermal cells which while separated from the cuticle, nevertheless remain embedded in the clypeus above the hymenium.

This appears to be an intermediate form between subcuticular and truly partly subepidermal ascocarps. When subcuticular, ascocarps of *L. molitoris* are similar in appearance to those of *L. nitens*, but have lips. *Lophodermium nitens* also has rounder conidiomata and is known only from haploxylon pines.

Literature: Minter (1980a). Publications treating '*L. nitens*' on diploxylon pines may refer to this species, e.g. Gordon (1966, 1968), Staley (1975b).

4. **Lophodermium baculiferum** Mayr, *Die Waldungen von Nordamerika*, p. 313, 1890. (Figs 4, 20, 40, 42, 49, 63, 64, 65)

Anamorph: *Leptostroma decipiens* Petr. (1922).

Diagnostic features: Ascocarps dark grey to black, subepidermal, without lips, splitting along a line of stomata; conidiomata subepidermal, coalescing laterally, ostioles not scattered over the surface; zone lines black, infrequent to abundant.

Ascocarps on secondary needles, on all sides, when wet shiny and black, when dry dark grey or black all over, with no perimeter line visible, but the outline being clearly marked, elliptical, raising the surface of the needle slightly, 600-1200μm long (clypeus extent), opening by a single longitudinal split along a line of stomata, lips absent; in mid-point vertical section subepidermal, the clypeus and basal wall being very well developed when mature, though the basal wall may be poorly developed in young ascocarps; in surface slice section aliform tissue is present in both the clypeus, where it is well developed, and the basal wall. *Paraphyses* hooked at the tips. *Asci* 90-170 $\times$ 10-15μm. *Ascospores* 90-130 $\times$ 2μm. *Conidiomata* on secondary needles, on all sides, grey to black, with a poorly defined outline, broadly to elongated elliptical, not or only slightly raising the needle surface, smooth, usually coalescing to form bilocular or more often multilocular conidiomata, the coalescing being mostly lateral, but also occasionally longitudinal, giving rise to multilocular conidiomata 200-700 $\times$ 150-400μm, with one to several inconspicuous ostioles in groups near the stomata which occur within the area of the needle occupied by the conidioma; in mid-point vertical section subepidermal; in surface slice section the upper wall extends over the whole conidioma, blackening being heavier near the stomata, the texture changing rapidly near the margin which is covered by a zone 15-30μm wide of aliform mycelium, ostioles visible as circular pores 8-15μm diameter in the upper wall, located below the cuticular covering around the stomata. *Conidiogenous cells* 8-12 $\times$ 2.5-4μm. *Conidia* rod shaped, 9-15 $\times$ 1μm. *Zone lines* black, infrequent to abundant.

Typification: Of *Lophodermium baculiferum*: on needles of *Pinus jeffreyi*, Lassen National Forest, Lassen County, California, U.S.A., 15 Aug. 1965, Lee Bonar, California Fungi 1273 (as *Lophodermium pinastri*), IMI 142151, neotype. Neotypified by Minter (1980a). The original collections of Mayr are lost fide Darker (1967).

Of *Leptostroma decipiens:* on needles of *Pinus ponderosa*, Missoula, Montana, U.S.A., 1914, J. R. Weir, Herb. J. R. Weir 9170, lectotype. Lectotypified by Thyr & Shaw (1964). The locality of the lectotype is not known, possibly W.

Selected specimens examined: On *P. jeffreyi*, Lassen National Forest, Lassen County, California, U.S.A., 15 Aug. 1965, Lee Bonar, IMI 142151, neotype of *Lophodermium baculiferum*; also IMI 23101, 228857; on *P. jeffreyi*, Gasquet, California, U.S.A., June 1933, H. E. Parks, (as *Lophodermium pinicolum*), K; on *P. ponderosa*, Siskyou County, California, U.S.A., 6 July 1903, E. B. Copeland, Pacific Slope Fungi 3583 (as *Lophodermium pinastri*), K.

Hosts: *Pinus jeffreyi, P. ponderosa, P. sabiniana.*

Distribution: North America: United States (California, Idaho, Montana, Washington, Wyoming).

Cultures: No information.

Fruiting period: No information.

Ecology: Known only from secondary needles of diploxylon pines of the *ponderosa* group.

Notes: The heavy blackening of the clypeus and lower wall in mature ascocarps of this species seen in vertical section is reminiscent of some loculoascomycetes.

Literature: Darker (1967), Mayr (1890), Minter (1980a), Petrak (1922), Thyr & Shaw (1964).

5. Lophodermium staleyi Minter sp. nov. (Figs 5, 21, 63, 64, 65)

Diagnostic features: Ascocarps small, black with a grey surround and black perimeter line, partly subepidermal, with grey lips; conidiomata subepidermal, ostioles not scattered over the surface; conidia $> 8\mu$m long; zone lines absent or black, rare.

Ascocarps on secondary needles, on all sides, when wet shiny and black, when dry black in the centre for more than half the total surface area, with a grey surround and black perimeter line making a clearly marked outline, elliptical, raising the surface of the needles slightly at the centre of the ascocarp, 350-800μm long (perimeter line), opening by a single longitudinal split, lips present, grey; in mid-point vertical section partly subepidermal, more than five epidermal cells being displaced and lying in a group on the basal wall, the clypeus becoming paler on either side and not extending as far as the basal wall which is poorly developed; in surface slice section aliform tissue is present in both the clypeus and the basal wall, but is poorly developed. *Paraphyses* tips straight and unswollen. *Asci* 70-115 $\times$ 9-12μm. *Ascospores* 65-95 $\times$ 2μm. *Conidiomata* bearing conidia 8-12 $\times$ 1μm, otherwise indistinguishable from those of *L. pinastri*. *Zone lines* absent or black, rare.

Hoc taxon ab aliis *Lophodermii* speciebus quae ascocarpos pro parte subepidermales et conidiomata omnino subepidermalia habeant differt non solum maiorem ob longitudinem conidiorum sed etiam quod ascocarpos minores habet.

Typification: On needles of *Pinus sylvestris*, Deskins Farm, Oregon, U.S.A., 16 Sept. 1973, C. S. Millar, IMI 225067, holotype.
Specimen examined: On *P. sylvestris*, Deskins Farm, Oregon, U.S.A., 16 Sept. 1973, C. S. Millar, holotype.
Hosts: *Pinus sylvestris*.
Distribution: North America: United States (Oregon).
Cultures: Slow growing, white, eventually in some cases producing thin black zone lines on the circumference. Very similar to cultures of *L. pinastri* and *L. pini-excelsae*, but with larger conidia, 8-12μm long, and growing more slowly than *L. pinastri* at 22°C.
Fruiting period: Ascocarps mature in January.
Ecology: Causes yellowing of 2-year-old secondary needles in late August.
Notes: *Lophodermium staleyi* is similar to *L. pinastri* and *L. pini-excelsae*. It differs from *L. pinastri* in having ascocarps on average only half as long, with lips which never bear the red pigment characteristic of *L. pinastri*, and in bearing conidia markedly longer. It differs from *L. pini-excelsae* in having ascocarps with more poorly developed basal walls, and in bearing conidia markedly larger, in conidiomata with more strongly developed upper walls. *Lophodermium staleyi* and *L. pini-excelsae* have been confused in the literature in the past: collections of *Lophodermium* with small grey lipped ascocarps maturing in January and February are known from Great Britain, and have in the past been identified as *L. pini-excelsae*; they are probably better placed in *L. staleyi*.

The epithet was chosen in recognition of the contribution made to the taxonomy of *Lophodermium* on pine by the forest pathologist J. M. Staley.
Literature: Minter (1980a), Minter, Staley & Millar (1978), Staley (1975b).

6. **Lophodermium pinastri** (Schrad. ex Hook.) Chev., *Flore générale des environs de Paris* **1**: 436, 1826. (Figs. 6, 22, 35, 36, 41, 47, 48, 55, 56, 63, 64, 65, Plate 1a, g)
≡*Hysterium pinastri* Schrad. (1799).
≡*Hysterium pinastri* Schrad. ex Hook. (1821).
≡*Hypoderma pinastri* (Schrad.) DC. (1805).
≡*Lophodermellina pinastri* (Schrad. ex Hook.) Höhn. (1917).
=*Hysterium limitatum* Wiebel (1799).
=*Lophodermium pinicolum* Tehon (1935).

Diagnostic features: Ascocarps black with a grey surround and black perimeter line, partly subepidermal, with lips often red; conidiomata subepidermal, ostioles not scattered over the surface; conidia < 7μm long; zone lines black, abundant.

Ascocarps on secondary needles, on all sides (>20% on adaxial or radial sides), when wet shiny and black, when dry black in the centre for more than half the total surface area, with a grey surround with a black perimeter line making a clearly marked outline, elliptical, raising the surface

of the needle slightly, 700-1200μm long (perimeter line), opening by a single longitudinal split, lips present, grey, red, orange, yellow or rarely when very wet green; in mid-point vertical section partly subepidermal, more than five epidermal cells being displaced and lying in a group on the basal wall, the clypeus becoming paler on either side and not extending as far as the basal wall which is poorly developed, specimens on needles of haploxylon pines sometimes having almost all the epidermal cells displaced and so appearing virtually subcuticular; in surface slice section aliform tissue is present in both the clypeus and the basal wall, but is poorly developed. *Paraphyses* tips usually straight and unswollen, sometimes hooked and/or swollen. *Asci* 110-155 $\times$ 9·5-11·5μm. *Ascospores* 70-110 $\times$ 2μm.

Conidiomata on secondary needles, on all sides, concolorous or greyish and slightly darker than the needle, with a darker, often well defined margin, elliptical to elongated elliptical, not or only slightly raising the needle surface, smooth, coalescing infrequently, 200-450 $\times$ 150-250μm, with or without ostioles, opening by a single longitudinal split to one side of the conidioma along a line of stomata, or between two rows of epidermal cells, ostioles when present being found in the blackened wall lining this split; in mid-point vertical section subepidermal; in surface slice section the upper wall extends over the whole conidioma, but is often poorly blackened and hard to see, the texture changing rapidly near the margin which is covered by a zone of aliform tissue which is however often poorly developed and may be absent, blackening being heavier near the stomata and split, and ostioles visible as circular pores 8-15μm diameter in the blackened wall lining the split. *Conidiogenous cells* 5-10 $\times$ 2-5μm. *Conidia* rod shaped, 4·5-6·25 $\times$ 1μm. *Zone lines* black, abundant.

Ascocarps on primary needles, on all sides, similar to those on secondary needles, but smaller, often more rounded, with almost all the epidermal cells displaced and so appearing virtually subcuticular. *Conidiomata* on primary needles, known to occur. *Zone lines* on primary needles, black, frequent.

Ascocarps on cones, on the apophyses, similar to those on secondary needles but smaller, often more rounded, opening with one longitudinal split or up to three radial splits, the depth of embedding being hard to determine because of the poorly defined cone epidermal cells. *Conidiomata* on cones, on the apophyses, known to occur. *Zone lines* on cones, black, frequent.

Typification: Mougeot & Nestler No. 76, the specimen of this exsiccatum in UC, neotype. Designated by Staley (1975b).

The typification of *L. pinastri* has been discussed by various authors, none satisfactorily. Tehon's (1935) proposal to typify *L. pinastri* with the exsiccatum Roumeguère, Fungi Gallici Exsiccati No. 1661 has never seriously been accepted (Lundell & Nannfeldt, 1936; Terrier, 1956). Darker (1932) considered a specimen cited by Fries (1823) should be type, and Tehon (1935) dealing with the same fungus under the name *L.*

pinicolum favoured the exsiccatum Fries, Scleromyceti Sueciae No. 50 (probably a misprint for 'No. 30'). Terrier (1956) and Staley (1975b) both favoured the exsiccatum Mougeot & Nestler No. 76 on the grounds that it was cited by Chevallier (1826). Staley's work is quoted in part here: 'I therefore amend Chevallier's citation by designating the specimen of M & N nr. 76 housed at the University of California, Berkeley as the type specimen of *L. pinastri* (Schrader ex Hooker) Chevallier. To further quiet argument and promote nomenclatural stability, I designate this same specimen as the neotype for *Hysterium pinastri* Schrader. A sufficient search by Dr. Maas Geesteranus of the royal herbarium at Leiden, has failed to indicate a more worthy specimen for this purpose.'

The type of a taxon, according to Article 7 of the International Code of Botanical Nomenclature (Stafleu et al., 1972), 'is to be determined in accordance with the indication or description and other matter accompanying the first valid publication. When valid publication is by reference to a pre-starting point description, the latter must be used for purposes of typification as though newly published.' In the case of *Lophodermium pinastri*, Hooker (1821) provided the first valid publication of the fungus as *Hysterium pinastri*, by taking up the pre-starting point description by Schrader (1799). Chevallier (1826) subsequently transferred the fungus to his new genus *Lophodermium* Chev. This is precisely what the term '(Schrad. ex Hook.) Chev.' implies. The specimens cited by Fries (1823) and Chevallier are thus totally irrelevant to the problem of typifying this species as they are not associated with the first valid publication, and Staley's designation of a type for *Lophodermium pinastri* (Schrad. ex Hook.) Chev. must be ignored as a mistake.

Since the epithet '*pinastri*' may be traced from the first valid publication by Hooker, back through Persoon (1801) to the pre-starting point author Schrader, it is clearly the best practice to use Schrader's description rather than Hooker's for purposes of typification. Schrader stated that the fungus occurred on leaves of *Pinus sylvestris* and *Pinus abies* (now *Picea abies*), but gave no further details of specimens. His illustration, reproduced below (Fig. 56) is clearly of a fungus on *P. sylvestris* producing black fruitbodies opening with a single longitudinal split and numerous black zone lines, and as such is easily identifiable. As Schrader mentioned material on more than one substrate, without indicating a preferred type, there can be no holotype. Schrader's specimens, together with the illustration, form the elements from which a lectotype should be selected. It is not known whether Schrader's specimens of *Hysterium pinastri* still exist. They are not in K, nor, fide Staley, in L, but may be in GOET or LE where some of his collections reside. Until they are discovered, the illustration accompanying the original publication is the only material which could serve as a lectotype. Unfortunately, although the fungus is clearly identifiable from the illustration, the absence of asci makes it unsuitable to be type material, as *L. pinastri* is a pleomorphic fungus (Article 59, Stafleu et al., 1972). There is thus at present no suitable lectotype, and Staley's neotype for *Hysterium pinastri* Schrad., which is the

same fungus as illustrated by Schrader, and which is a widely distributed exsiccatum cited by most of the earliest authors, and for which many isoneotypes are available, should be accepted.

Selected specimens examined: Mougeot & Nestler No. 76, K, isoneotype; Mougeot & Nestler No. 76, E, isoneotype; IMI 11604, 11840, 23116, 156241, 231808, 234406, 234613, 238368, 239381, 243685, 243694, 247600; on cones: IMI 231791, 231806, 233580.

Hosts: *Pinus armandi*[0], *P. attenuata*[0], *P. austriaca*, *P. ayacahuite*[0], *P. banksiana*[0], *P. brutia*, *P. canariensis*[0], *P. cembra*, *P. contorta* var. *contorta*[0], *P. contorta* var. *latifolia*[0], *P. coulteri*[0], *P. densiflora*[0], *P. durangensis*[0], *P. elliottii*[0], *P. engelmanii*[0], *P. greggii*[0], *P. halepensis*, *P. koraiensis*[0], *P. leiophylla*[0], *P. leucodermis*, *P. massoniana*[0], *P. montana*, *P. montezumae*[0], *P. monticola*[0], *P. mugo*, *P. muricata*[0], *P. nigra* var. *maritima*, *P. nigra* var. *nigra*, *P. palustris*[0], *P. parviflora*[0], *P. pinaster*, *P. pinea*, *P. ponderosa*[0], *P. pumila*[0], *P. radiata*[0], *P. resinosa*[0], *P. rigida*[0], *P. sibirica*, *P. strobus*[0], *P. sylvestris*, *P. tabuliformis*[0], *P. thunbergii*[0], *P. uncinata*, *P. wallichiana*[0].

Distribution: Asia: Japan[0], U.S.S.R. (Krasnoyarsk). Australasia: Australia (Capital Territory[0], Tasmania[0]), New Zealand[0]. Europe: Austria, Belgium, Czechoslovakia, Denmark, Finland, France, Germany, Great Britain, Greece, Holland, Ireland, Italy, Poland, Romania, Spain, Switzerland, U.S.S.R. (Latvia), Yugoslavia. North America: Canada (Ontario[0]), United States (Maine[0], Michigan[0], Oregon[0], Washington[0]).

Cultures: Slow growing, compact, white, growth ceasing before the edge of the dish is reached, producing thin black zone lines on the circumference, sometimes also black crusts on the surface, conidia often abundant, 4·5-6·25μm long. Indistinguishable from cultures of *L. pini-excelsae*, very similar to cultures of *L. staleyi*, but growing more rapidly at 22°C and with shorter conidia.

Fruiting period: In Scotland on secondary needles of *P. sylvestris* conidiomata appear from November to January, maturing from December to January and remaining visible for many months; zone lines appear from November to January and remain visible for many months; ascocarps appear from December to April, opening from about March to July, and releasing ascospores from April to August (Minter & Millar, 1980a). This periodicity is probably general throughout most of Europe. The fruiting periods on primary needles and cones are not known.

Ecology: In Scotland *L. pinastri* can be isolated from apparently healthy green secondary needles of *P. sylvestris* and *P. nigra*, but causes no damage. It mostly fruits on senesced secondary needles which have fallen to the litter (habitat category 1). It has also been recorded from secondary needles of habitat category 2 which were senescent at the time of death, and from secondary needles in habitat category 4 following attack by *Lophodermella sulcigena* (Minter & Millar, 1980a). This ecology is probably general throughout most of Europe, and has also been reported for *L. pinastri* in regions where it is not native (Stahl, 1966; Staley, 1975b). The ecology on primary needles and cones is not known.

Notes: Possibly the commonest *Lophodermium* on pines in Europe. Most literature about *Lophodermium* on pines purports to concern this species but usually in fact concerns other species, or a mixture of species. As *L. pinastri* appears to cause no harm to pines in Europe, the literature on the damage it causes and its control is particularly suspect, and usually refers to other species, probably mostly *L. seditiosum*. In the list of selected literature below, references are given only to papers in which *L. pinastri* is recognisable as understood here; even in most of these papers caution is advised.

Selected literature: Cultures: Langner (1933), Lanier (1968b, 1969), Lanier & Hubbes (1969), Millar & Richards (1975), Millar & Watson (1971), Minter (1977), Minter & Millar (1980b⁰), Staas-Ebregt & Gremmen (1975), Staley (1975b), Stephan (1973a, 1973b, 1975⁰).

Development & Physiology: Gordon (1966, 1968), Jones (1935⁰), Lanier & Hubbes (1969), Morgan-Jones & Hulton (1979⁰), Rack (1959a), Stephan (1969a, 1969b, 1973a, 1973b, 1975⁰).

Ecology & Fruiting periods: Lanier (1967a, 1968b, 1969, 1970), Lanier & Aussenac (1969), Lanier & Sylvestre (1971), Lanier & Zeller (1968), Lanier, Zeller & Zeller (1969), Millar & Richards (1975⁰), Minter (1977), Minter & Millar (1980a⁰), Mitchell & Millar (1978a, 1978b), Mitchell, Millar & Minter (1978), Stahl (1966), Staley (1975b), Watson (1971).

Nomenclature & Typification: Chevallier (1826), Darker (1932, 1967), Hooker (1821), Lundell & Nannfeldt (1936), Minter (1977), Persoon (1801), Schrader (1799), Staley (1975b), Tehon (1935), Terrier (1956).

On Cones: Butin (1975⁰).

Leptostroma stage: Minter (1980a⁰).

7. **Lophodermium indianum** Singh & Minter sp. nov. (Figs 7, 23, 63, 64, 65)

Diagnostic features: Ascocarps black with a grey surround and black perimeter line, partly sybhypodermal, with grey lips; conidiomata absent; zone lines black, infrequent to frequent.

Ascocarps on secondary needles, on all sides but mainly on the abaxial side, when wet shiny and black, when dry black in the centre for about a quarter of the total surface area, with a surround grey or concolorous with the needle surface and a black perimeter line making a clearly marked outline, elliptical or slightly pointed at each end, raising the surface of the needle slightly, 700-1100μm long (perimeter line), opening by a single longitudinal split, lips present, grey; in mid-point vertical section partly subhypodermal, one to four epidermal cells being displaced and lying scattered or in a group above the displaced hypodermal cells on the basal wall, some specimens being known where no epidermal cells are displaced and only hypodermal cells lie on the basal wall, the clypeus becoming paler on either side and not extending as far as the basal wall which is well

developed; in surface slice section aliform tissue is present in the basal wall. *Paraphyses* tips slightly swollen and bent. *Asci* 80-130 × 9-12μm. *Ascospores* 70-100 × 2μm. *Conidiomata* not observed. *Zone lines* black, infrequent to frequent.

Hoc taxon a *L. australi* differt quod ascocarpos habet muro basali indutos et lineas zonales nigras; ab aliis *Lophodermii* speciebus quae pini acus incolant differt quod ascocarpis pro parte subhypodermalibus gaudet.

Typification: On needles of *Pinus roxburghii*, Fri, U.P., India, June 1979, S. Singh, IMI 247571, holotype.

Specimens examined: On *P. roxburghii*, Fri. U.P., India, June 1979, S. Singh, IMI 247571, holotype; also IMI 247568, 247569, 247570, 247588, 248400, 248401, 248402, 248403, 248404, 248405.

Hosts: *Pinus caribaea*^{0}, *P. glabra*, *P. patula*, *P. roxburghii*, *P. serotina*, *P. taeda*^{0}, *P. thunbergii*^{0}.

Distribution: Asia: India.

Cultures: No information.

Fruiting period: No information.

Ecology: Known only from secondary needles from, at least in some cases, the litter.

Notes: *Lophodermium indianum* appears to be common in India. It is most similar in external appearance to *L. pinastri* on account of the black zone lines, but differs in being partly subhypodermal and in apparently lacking a conidial stage. Ascocarps of *L. conigenum* often look similar, but are not associated with black zone lines. Ascocarps of *L. australe* are embedded to a similar depth, but lack a basal wall.

Literature: None.

8. Lophodermium conigenum (Brunaud) Hilitz., *Vědecké Spisy vydávané Československou Akademií Zemědělskou* **3:** 76, 1929. (Figs 8, 24, 35, 45, 46, 51, 52, 57, 58, 59, 63, 64, 65, Plate 1h)

≡*Lophodermium pinastri* forma *conigena* Brunaud (1888).

≡*Lophodermium conigena* (Brunaud) Tehon (1935).

Anamorph: *Leptostroma pinorum* Sacc. (1882).

Diagnostic features: Ascocarps large, black with a grey surround and black perimeter line, partly subepidermal, with green lips; conidiomata subepidermal, ostioles in the centre of the surface; zone lines absent or brown, infrequent.

Ascocarps on secondary needles, on all sides (< 20% on adaxial or radial sides), when wet shiny and black, when dry black in the centre for less than a quarter of the total surface area, with a grey surround with a black perimeter line making a clearly marked outline, elliptical or more often pointed at each end, raising the surface of the needle slightly, 900-2000μm long (perimeter line), opening by a single longitudinal split, lips present, grey, green, fawn, rarely reddish when old and dry; in mid-point vertical section partly subepidermal, less than seven epidermal cells being

displaced and lying scattered over the basal wall, the clypeus becoming paler on either side and not extending as far as the basal wall which is poorly developed; in surface slice section aliform tissue is present in both the clypeus and the basal wall, but is poorly developed. *Paraphyses* tips sometimes straight and unswollen, sometimes hooked and/or swollen. *Asci* 160-215 × 11·5-14μm. *Ascospores* 90-130 × 2μm.
Conidiomata on secondary needles, on all sides, concolorous or greyish and slightly darker than the needle, with a darker poorly defined margin, elongated elliptical, not or only slightly raising the needle surface, smooth, 300-550 × 200-280μm, frequently coalescing, mostly longitudinally, to form bilocular or more often multilocular conidiomata up to about 1cm long, with one to several ostioles appearing as a dark spot or cluster of spots more or less in the centre of the surface of each locule, sometimes also opening by a single longitudinal split to one side of the conidioma along a line of stomata, or between two rows of epidermal cells; in mid-point vertical section subepidermal; in surface slice section the upper wall may extend over the whole conidioma, but is usually limited to an area within a radius of about 30μm from the nearest ostiole, and to a region about 20μm wide marking the edge of the conidioma, the blackening being heavier near ostioles and splits, ostioles being visible as circular pores 8-15μm diameter in the upper wall. *Conidiogenous cells* 5-10×2-4μm *Conidia* rod shaped, 4·5-9·5 × 1μm. *Zone lines* brown, infrequent.

Ascocarps on cones, on the apophyses, similar to those on secondary needles but smaller, often more rounded, opening with one longitudinal split or up to three radial splits, the depth of embedding being hard to determine because of the poorly defined cone epidermal cells. *Conidiomata* on cones, on the apophyses, known to occur. *Zone lines* on cones, brown, infrequent.

On secondary needles three varieties of the anamorph can be recognised (Fig. 55):

Leptostroma pinorum var. **pinorum**
Conidiomata markedly coalescing longitudinally. *Conidia* 6·25-9·5 × 1μm. Usually on *Pinus pinaster*.

Leptostroma pinorum var. **cembrae** (Bubák & Kabát) Minter, *Canadian Journal of Botany* **58**: 912, 1980.
≡*Leptostroma pinastri* var. *cembrae* Bubák & Kabát (1915).
Conidiomata less elongated and coalescing less frequently than var. *pinorum* *Conidia* 6·25-9·5 × 1μm. On *Pinus cembra*.

Leptostroma pinorum var. **graupianum** Minter var. nov.
Conidiomata coalescing longitudinally but less markedly so than var. *pinorum*. *Conidia* 4.5-8.25 × 1μm. On *Pinus* species other than *P. pinaster* and *P. cembra*.

Haec varietas differt brevioria ob conidia.
Typification: Of *Lophodermium conigenum:* on needles of *Pinus sylvestris*, Glentanar, Aberdeenshire, Scotland, 5 Sept. 1975, C. S. Millar, IMI 231805, neotype.

The typification of *L. conigenum* has been discussed by Minter (1977) and Minter et al. (1978), but not satisfactorily. Hilitzer (1929) clearly indicated that in using the epithet '*conigenum*' he was raising Brunaud's (1888) form to specific status. Hilitzer's collections are thus not relevant, as Minter et al. (1978) had supposed, to the problem of typification, because they did not accompany the first valid publication of the epithet '*conigenum*' (article 7). The first valid publication was by Brunaud (1888) who cited a collection 'sur les écailles des cônes du *Pinus silvestris*.—La Mothe-Saint-Heray.—RICHARD'. Staley (pers. comm.) attempted to locate this collection and was informed that all Brunaud's material had been 'given the broom'. It thus seems unlikely that any original material will turn up, and the selection of a neotype is therefore necessary.

The neotype designated above was chosen to ensure that *Lophodermium conigenum* continues to be used in the sense that recent workers have used the name (Minter et al., 1978; Minter & Millar, 1978a, 1980a, 1980b; Minter 1980a). To achieve this, it has been necessary to neotypify with a specimen on needles and not on cones. Although this apparently contradicts the original description, experience has shown that species of *Lophodermium* which fruit on needles and cones are easier to distinguish on needles, so that specimens on needles are far more suited for typification.

Of *Leptostroma pinorum* var. *pinorum*: On needles of *Pinus* sp., Brionne, Malbranche, France, Herb. P. A. Saccardo, PAD, holotype. The pine is probably *P. pinaster*.

Of *Leptostroma pinorum* var. *cembrae*: On needles of *Pinus cembra*, Monte Ciampedie, Fassathale, South Tyrol, Austria, 20 Aug. 1913, J. E. Kabát, K, lectotype. In the original description, Bubák & Kabát (1915) cited specimens on needles of *P. cembra* from 'der Regensburger Hütte in Gröden und am Monte Ciampedie in Fassatale', but indicated no preference for a type. Part of their collection from Monte Ciampedie in Fassathale is present in K, and is here selected as lectotype.

Of *Leptostroma pinorum* var. *graupianum*: On needles of *Pinus sylvestris*, Tarland, Aberdeenshire, Scotland, 17 Feb. 1975, D. W. Minter, IMI 231777, holotype.

Selected specimens examined: On *P. sylvestris*, Glentanar, Aberdeenshire, Scotland, 5 Sept. 1975, C. S. Millar, IMI 231805, neotype of *Lophodermium conigenum*; on *Pinus* sp., Brionne, Malbranche, France, Herb. P. A. Saccardo, PAD, holotype of *Leptostroma pinorum* var. *pinorum*; on *P. cembra*, Monte Ciampedie, Fassathale, South Tyrol, Austria, 20 Aug. 1913, J. E. Kabát, K, lectotype of *Leptostroma pinorum* var. *cembrae*; on *P. sylvestris*, Tarland, Aberdeenshire, Scotland, 17 Feb. 1975, D. W. Minter, IMI 231777, holotype of *Leptostroma pinorum* var. *graupianum*; also IMI 224112, 225121, 225123, 225871, 227212, 227215, 231787, 234620, 238648, 238672, 238676, 239355, 241497, 243701; on cones: on *P. uliginosa*, Černe Jesero, Šumava, Czechoslovakia, 5 Oct. 1927, A. Hilitzer, PRM 705180 (as *Lophodermium squamicolum* ined.); also IMI 67978, 237369, 243784.

Hosts: *Pinus aristata*[0], *P. attenuata*[0], *P. ayacahuite*[0], *P. banksiana*, *P. brutia*, *P. cembra*, *P. contorta* var. *contorta*[0], *P. densiflora*[0], *P. halepensis*, *P. holfordiana*[0], *P. maritima*, *P. montana*, *P. mugo*, *P. muricata*[0], *P. nigra*, *P. peuce*, *P. pinaster*, *P. pinea*, *P. ponderosa*[0], *P. pumila*[0], *P. radiata*[0], *P. resinosa*[0], *P. rigida*[0], *P. sylvestris*, *P. tabuliformis*[0], *P. uliginosa*, *P. virginiana*[0].

Distribution: Africa: Azores. Australasia: New Zealand[0]. Europe: Austria, Belgium, Czechoslovakia, Denmark, France, Germany, Great Britain, Greece, Holland, Italy, Poland, Portugal, Sweden, Yugoslavia. North America: Canada (Ontario), United States (Massachusetts, Maryland, Michigan, New Jersey).

Cultures: Fast growing, fluffy, white later sometimes becoming tan or occasionally brown, with swirling appearance when young, growth usually continuing until the edge of the dish is reached, sometimes producing brown diffuse zone lines on the circumference, conidia produced abundantly only on sterilised needles placed on the cultures, the same size as in vivo. Cultures of the *Leptostroma* varieties with longer conidia are indistinguishable from those of *Lophodermium australe*. Cultures of the *Leptostroma* variety with shorter conidia differ only slightly in conidia length from cultures of *Lophodermium seditiosum* and may be hard to distinguish particularly when brown.

Fruiting period: In Scotland on secondary needles of *P. sylvestris* conidiomata appear from July to December, maturing from August to December and remaining visible for many months; zone lines appear from July to August and remain visible for many months; ascocarps appear from August to September, opening from October to December, and releasing ascospores from October to June with a peak between November and February (Minter & Millar, 1980a). This periodicity is probably general throughout most of Europe. The fruiting periods on primary needles and cones are not known.

Ecology: In Scotland *L. conigenum* can be isolated from apparently healthy green secondary needles of *P. sylvestris* and *P. nigra*, but causes no damage. It mostly fruits on secondary needles on trash (habitat category 2). It has also been recorded from secondary needles in habitat category 3, and from secondary needles in habitat category 4 following attack by *Lophodermella sulcigena* (Minter & Millar, 1980a). The fungus appears often to be absent from isolated stands of pine, particularly on islands (Minter, 1980b). This ecology may be general in much of Europe, but in Czechoslovakia *L. conigenum* has also been observed fruiting on dead needles attached to dead shoots on living trees of *P. mugo*. The ecology on cones is not known, although *L. conigenum* is not rare in this habitat.

Notes: In the list of selected literature below, references are given only to papers in which *L. conigenum* is recognisable as understood here.

Selected literature: Brunaud (1888), Bubák & Kabát (1915), Butin (1975), Hilitzer (1929), Millar & Richards (1975[0]), Minter (1977, 1980a[0]) Minter & Millar (1978a, 1980a[0], 1980b[0]), Minter Staley & Millar (1978), Reid & Minter (1979), Stephan (1973a, 1973b, 1975[0]).

9. Lophodermium australe Dearn., *Mycologia* **18:** 242-243, 1926. (Figs. 9, 25, 50, 63, 64, 65)

Anamorph: *Leptostroma durissimum* Cooke (1878).

Diagnostic features: Ascocarps thin, black sometimes with a faint grey surround but without a perimeter line, partly subepidermal or partly subhypodermal, with lips; conidiomata subepidermal, ostioles in the centre of the surface; zone lines absent.

Ascocarps on secondary needles, on all sides but mainly on the abaxial side, when wet elongated elliptical, black and pointed at each end, when dry appearing as a thin black line between two rows of stomata, sometimes with a faint grey surround, but without a perimeter line and so with a poorly marked outline when the grey surround is present, not raising the surface of the needle, 500-2000μm long (clypeus extent), opening by a single longitudinal split, lips present, grey; in mid-point vertical section partly subepidermal, less than five epidermal cells being displaced and lying scattered below the ascocarp, or partly subhypodermal, the displaced hypodermal cells lying in a group below the centre of the ascocarp, and less than five epidermal cells being displaced and lying scattered below the ascocarp, the clypeus becoming paler on either side with little or no pigmented basal wall visible; in surface slice section aliform tissue is present in the clypeus. *Paraphyses* tips sometimes straight and unswollen, sometimes hooked and/or swollen. *Asci* 65-150 $\times$ 8-12μm. *Ascospores* 55-120 $\times$ 2μm. *Conidiomata* differing from those of *L. conigenum* by coalescing less frequently and by opening more frequently by a longitudinal split to one side of the conidioma. *Conidia* rod shaped, 6·25-9 $\times$ 1μm. *Zone lines* absent.

Typification: Of *Lophodermium australe*: on needles of *Pinus palustris*, Silver Springs, Florida, U.S.A., 27 Feb. 1919, G. G. Hedgcock, Herb. G. G. Hedgcock 32146, DAOM, lectotype.

Dearness cited over forty collections of *L. australe* in his original description, giving detailed information and accession numbers for two. Of these two, the collection cited above has been designated lectotype here as it is clearly the collection other workers have considered to be the type of this species. Darker (1932) concluded that this type was merely a combination of immature *Lophodermium pinastri* and *Ploioderma lethale* (Dearn.) Darker. In a note enclosed with the specimen, Staley remarked that some *Davisomycella medusa* (Dearn.) Darker was present with the *Lophodermium*. Whatever the identity of the other fungus, the *Lophodermium* present is consistent with Dearness' description and is undoubtedly different from *L. pinastri*.

Of *Leptostroma durissimum*: on needles of *Pinus* sp., Aiken, South Carolina, U.S.A., 2433, Herb. M. C. Cooke, K, holotype.

Selected specimens examined: On *P. palustris*, Silver Springs, Florida, U.S.A., 27 Feb. 1919, G. G. Hedgcock, Herb. G. G. Hedgcock 32146, DAOM, lectotype of *Lophodermium australe*; on *P. taeda*, Brooksville, Florida, U.S.A., 3 Dec. 1915, G. G. Hedgcock, Herb. G. G. Hedgcock

17436, DAOM, syntype of *Lophodermium australe*; on *Pinus* sp., Aiken, South Carolina, U.S.A., 2433, Herb. M. C. Cooke, K, holotype of *Leptostroma durissimum*; also IMI 23102, 84368, 115619, 156989, 164169c, 166132, 168714, 179652, 187034, 193278, 238671, 238673, 238675, 239350, 247604, 247605, 247606, 247608.

Hosts: *Pinus australis*, *P. caribaea* var. *caribaea*, *P. caribaea* var. *hondurensis*, *P. echinata*, *P. elliottii*, *P. insularis*, *P. palustris*, *P. patula*, *P. pinaster*, *P. rigida*, *P. taeda*.

Distribution: Africa: Zambia[0]. Asia: Malaysia[0], Philippines[0], Selangor[0]. Australasia: Australia[0], Fiji[0]. North America: Jamaica, Mexico, United States (Alabama; Florida, Georgia, Hawaii[0], Louisiana, North Carolina, South Carolina). South America: Belize, Brazil[0], Honduras.

Cultures: Fast growing, fluffy, white later sometimes becoming tan or occasionally brown, with swirling appearance when young, growth usually continuing until the edge of the dish is reached, conidia produced abundantly only on sterilised needles placed on the cultures, the same size as in vivo. Indistinguishable from cultures of varieties of *Lophodermium conigenum* with longer conidia.

Fruiting period: No information.

Ecology: Known only from secondary needles. Saprophytic and very common on foliage left in pine forests after harvesting in the southern U.S.A. (Staley, 1975b), also known from litter and may be pathogenic in some circumstances (Bega et al., 1978).

Notes: *Lophodermium australe* and *L. conigenum* are clearly quite closely related. When ascocarps of *L. australe* have no pigmented basal wall they are not difficult to distinguish from ascocarps of *L. conigenum*, but ascocarps with poorly defined basal walls are often very difficult to identify satisfactorily, and it seems likely that the two species intergrade.

Literature: Bega et al. (1978), Czabator, Staley & Snow (1971), Gibson (1979), Minter (1977, 1980a[0]), Minter & Millar (1978a), Staley (1975b[0]).

10. Lophodermium ravenelii Minter sp. nov. (Figs. 10, 26, 54, 63, 64, 65)

Diagnostic features: Ascocarps totally grey without a clearly defined perimeter line, totally subepidermal, with lips; conidiomata subepidermal, ostioles not in the centre of the surface; conidia $> 15\mu$m long; zone lines brown, infrequent to frequent.

Ascocarps on secondary needles, on all sides, when wet shiny and black, when dry grey (though often with black spots marking the location of the needle stomata), without a clearly defined perimeter line, and so without a clearly defined margin, elongated elliptical and often rather pointed at each end, raising the surface of the needle slightly, 750-1100μm long (clypeus extent), opening by a single longitudinal split, lips present, grey; in mid-point vertical section totally subepidermal (although stoma cells may be displaced), the clypeus extending on either side as far as the basal

wall which is poorly developed; in surface slice section aliform tissue is present in the upper wall, but is poorly developed. *Paraphyses* tips sometimes straight and unswollen, sometimes hooked and/or swollen. *Asci* 80-110 × 10-13μm. *Ascospores* 70-100 × 2μm.

Conidiomata on secondary needles, on all sides, concolorous or grey to dark grey, sometimes with a darker, often well defined margin, elliptical to elongated elliptical, not or only slightly raising the needle surface, smooth, coalescing infrequently, 200-450μm long, ostioles not observed, opening by a single longitudinal split to one side, or by two longitudinal splits one on each side of the conidioma along a line of stomata, or between two rows of epidermal cells; in mid-point vertical section subepidermal; in surface slice section the upper wall extends over the whole conidioma, but is often poorly blackened and hard to see, the texture changing rapidly near the margin which is covered by a zone of aliform tissue which is usually only clearly seen in the heavier blackened region lining the split. *Conidiogenous cells* 4-9 × 2-4μm. *Conidia* threadlike, 15-22 × 1μm. *Zone lines* brown, infrequent to frequent.

Hoc taxon ascocarpos habet omnino subepidermales, sed ab aliis taxis quae ascocarpos similes producant differt longitudinem ob conidiorum.

Typification: On needles of *Pinus* sp., Houston, Texas, U.S.A., 12 April, H. W. Ravenel, herb. Ravenel No. 188, K, holotype.

Specimens examined: On *Pinus* sp., Houston, Texas, U.S.A., 12 April, H. W. Ravenel, herb. Ravenel No. 188, K, holotype; on *Pinus* sp., South Carolina, U.S.A., spring, H. W. Ravenel, herb. Ravenel No. 653, K; several other collections by Ravenel in K are also probably of this species.

Hosts: *Pinus* sp.

Distribution: North America: United States (South Carolina, Texas).

Cultures: No information.

Fruiting period: No information.

Ecology: No information.

Notes: Although rather similar to *L. seditiosum*, this species may be easily distinguished by its exceptionally long conidia. It is strange that there appear to be no recent collections.

Literature: None.

11. Lophodermium seditiosum Minter, Staley & Millar, *Transactions of the British Mycological Society* **71**: 300, 1978. (Figs. 11, 27, 33, 35, 53, 55, 63, 64, 65, Plate 1b, c, i)

=*Lophodermium pinastri* auct.

Anamorphs: *Leptostroma austriacum* Oud. (1904), the anamorph on primary needles only.

Leptostroma rostrupii Minter (1980a), the anamorph on secondary needles only.

≡*Depazea linearis* Rostrup (1883).

Non *Leptostroma lineare* Lév.

Diagnostic features: Ascocarps totally grey, often with a black perimeter line, totally subepidermal, with blue or green lips; conidiomata sub-

epidermal, ostioles in the centre of the surface; zone lines absent or brown, infrequent.

Ascocarps on secondary needles, on all sides (< 20% on adaxial or radial sides), when wet shiny and black, when dry grey often with a black perimeter line making a clearly marked outline, elliptical or more often pointed at each end, raising the surface of the needle slightly, 800-1600μm long (perimeter line), opening by a single longitudinal split, lips present, grey, blue or green; in mid-point vertical section totally subepidermal, the clypeus becoming paler on either side and not extending as far as the basal wall which is poorly developed; in surface slice section aliform tissue is present in both the clypeus and the basal wall, but is poorly developed. *Paraphyses* tips sometimes straight and unswollen, sometimes hooked and/or swollen. *Asci* 140-170 × 11-13·5μm. *Ascospores* 90-120 × 2μm. *Conidiomata* differing slightly in conidia lengths (Fig. 55) otherwise indistinguishable from *Leptostroma pinorum* var. *pinorum* and *L.pinorum* var. *graupianum*, but more elongated than *L. pinorum* var. *cembrae*. *Zone lines* brown, infrequent.

Ascocarps on primary needles known to occur, possibly 'intraepidermal' fide Staley (1975b). *Conidiomata* on primary needles similar to those of *Lophodermium nitens* on secondary needles, but more or less elliptical, frequently coalescing to form bilocular or multilocular conidiomata. *Zone lines* on primary needles, not observed.

Ascocarps on cones, on the apophyses, similar to those on secondary needles but smaller, often more rounded, opening with one longitudinal split or up to three radial splits, the depth of embedding being hard to determine because of the poorly defined cone epidermal cells, lips often characteristically blue. *Conidiomata* on cones, on the apophyses, elliptical, black, subcuticular or embedded under degraded elements of the epidermal cells, similar in structure to the conidiomata on primary needles. *Zone lines* on cones, brown, infrequent.

Typification: Of *Lophodermium seditiosum*: on needles of *Pinus sylvestris*, Gray's Harbor County, Washington, U.S.A., Sept. 1973, C. S. Millar & J. M. Staley, IMI 225142, holotype.

Of *Leptostroma austriacum*: on primary needles of *Pinus austriaca*, Schoorl, Amsterdam, Netherlands, 12 June 1904, J. Ritzema Bos, L, holotype.

Of *Leptostroma rostrupii*: on secondary needles of *Pinus sylvestris* (eight collections), on secondary needles of *P. montana* (two collections), on secondary needles of *P. austriaca* (five collections), herb. E. Rostrup, C. In his description of *Depazea linearis* Rostrup cited no specimens, but provided an illustration which can serve as lectotype. If the illustration were considered inadequate, a neotype could be chosen, preferably from among the fifteen specimens of *D. linearis* in Rostrup's herbarium, cited above.

Selected specimens examined: On *P. sylvestris*, Gray's Harbor County, Washington, U.S.A., Sept. 1973, C. S. Millar & J. M. Staley, IMI 225142, holotype of *Lophodermium seditiosum*; illustration of *Depazea linearis* in Rostrup (1883), lectotype of *Leptostroma rostrupii*; on *P. sylvestris* (eight

collections), on *P. montana* (two collections), on *P. austriaca* (five collections), identified as *Depazea linearis*, herb. E. Rostrup, C; isotypes of *Lophodermium seditiosum* in FPF (4436) and PRM; also IMI 17514, 94248, 156239, 214290, 225068, 225069, 225070, 225071, 225072, 225138, 225139, 225140, 225141, 225384, 231786, 238674, 239353; on primary needles: on *P. austriaca*, Schoorl, Amsterdam, Netherlands, 12 June 1904, J. Ritzema Bos, L, holotype of *Leptostroma austriacum*; on cones: IMI 89615b, 225383, 241502, 241504, 241506.

Hosts: *Pinus austriaca*, *P. cembra*, *P. contorta* var. *contorta*[0], *P. contorta* var. *latifolia*[0], *P. densiflora*[0], *P. durangensis*[0], *P. halepensis*, *P. montana*, *P. montezumae*[0], *P. nigra* var. *nigra*, *P. nigra* var. *maritima*, *P. palustris*[0], *P. resinosa*[0], *P. sylvestris*, *P. virginiana*[0].

Distribution: Europe: Austria, Belgium, Czechoslovakia, Finland, France, Germany, Great Britain, Greece, Holland, Hungary, Ireland, Poland, Switzerland, U.S.S.R. (Latvia), Yugoslavia. North America: United States (Indiana[0], Michigan[0], Oregon[0], Washington[0]).

Cultures: Fast growing, fluffy, white later almost always becoming tan or more often brown, with swirling appearance when young, growth usually ceasing before the edge of the dish is reached, sometimes producing brown diffuse zone lines on the circumference though these are usually hard to distinguish on account of the brown colour of the colony, conidia produced abundantly only on sterilised needles placed on the cultures, the same size as in vivo. Hard to distinguish when pale from cultures of *Leptostroma pinorum* var. *graupianum*.

Fruiting period: In Scotland on secondary needles of *P. sylvestris* conidiomata appear from May to October and remain visible for many months; zone lines appear in June and remain visible for many months; ascocarps appear from June to October, opening from August to December, and releasing ascospores from August to May with a peak between October and January (Minter & Millar, 1980a). This periodicity is probably general throughout the range of *L. seditiosum* (Minter & Millar, 1980a). The fruiting periods on primary needles and cones are not known.

Ecology: In Scotland *L. seditiosum* can be isolated from apparently healthy green secondary needles of *P. sylvestris* and *P. nigra*, causing no damage, or associated on *P. sylvestris* with needlecast disease of which it is probably the cause. In cases of needlecast disease (habitat category 5), *L. seditiosum* fruits on secondary needles which it has killed while still attached to young plants, the needles being in their second year at the time of fruiting. *Lophodermium seditiosum* also fruits on secondary needles on trash (habitat category 2), very sparsely when *L. conigenum* is also present on the trash, but sometimes abundantly when *L. conigenum* is absent (Minter, 1980b), in which case the trash can be a significant source of inoculum sufficient to trigger off a needlecast outbreak (Murray & Young, 1956). The ecology on primary needles and cones is not known, although *L. seditiosum* is sometimes abundant on cones.

Notes: Examination of the literature on needlecast disease shows that almost all outbreaks attributed to *Lophodermium*, and almost all the literature on the control of these outbreaks relates to *L. sediotisum* and not to *L. pinastri*. The name *L. pinastri* has however been used mistakenly in much of this literature. In the list of selected literature below, references are given only to papers in which *L. seditiosum* is recognisable as understood here; even in most of these papers caution is advised.

It is interesting to note that the *Leptostroma* stage of *L. seditiosum* differs in depth of embedding between secondary needles and primary needles and cones. When on secondary needles, the depth of embedding is remarkably constant, and is subepidermal, with the name *Leptostroma rostrupii*. On primary needles (and cones) it is subcuticular, with the name *Leptostroma austriacum*. It must be very unusual for a pleomorphic fungus to have two anamorphs in the same form genus.

Selected literature: Kurkela (1979⁰), Merrill & Kistler (1977), Millar & Richards (1975), Minter (1980a⁰, 1980b), Minter & Jančařík (1980), Minter & Millar (1978a, 1980a⁰, 1980b⁰), Minter, Staley & Millar (1978⁰), Murray & Young (1956), Nicholls (1973), Nicholls & Skilling (1970, 1972, 1974), Oudemans (1904), Pagony (1963, 1964, 1970), Rack (1955), Rostrup (1883), Skilling & Nicholls (1971, 1975), Staas-Ebregt & Gremmen (1975), Staley (1975a⁰, 1975b⁰), Stephan (1973a⁰, 1973b⁰, 1975⁰).

12. **Lophodermium pini-excelsae** Ahmad, *Sydowia* 8: 172-173, 1954. (Figs. 12, 28, 63, 64, 65)

Diagnostic features: Ascocarps small, black with a dark grey surround and black perimeter line, partly subepidermal, with grey lips; conidiomata subepidermal, upper wall very poorly developed, ostioles in the centre of the surface; conidia $< 8\mu$m long; zone lines absent or black, rare.

Ascocarps on secondary needles, on all sides but mainly on the abaxial side, when wet shiny and black, when dry black in the centre for more than half the total surface area, with a dark grey to grey surround and black perimeter line making a clearly marked outline, elliptical, raising the surface of the needles slightly at the centre of the ascocarp, 300-800μm long (perimeter line), opening by a single longitudinal split, lips present, grey; in mid-point vertical section partly subepidermal, often more, sometimes less than five epidermal cells being displaced and lying in a group on the basal wall, sometimes even totally subepidermal, the clypeus sometimes becoming paler on either side and not extending as far as the basal wall, but often being well developed and extending on either side as far as the basal wall which is well to poorly developed; in surface slice section aliform tissue is present in both the clypeus and the basal wall, and may be well developed. *Paraphyses* tips variable, usually straight and unswollen. *Asci* 80-130 $\times$ 10-12μm. *Ascospores* 50-75 $\times$ 2μm.

Conidiomata on secondary needles, on all sides but mainly on the abaxial

side, the same colour as, or slightly paler than the needle, sometimes with a darker margin, elliptical to elongated elliptical, not or only slightly raising the needle surface, smooth, coalescing infrequently, 150-350μm long, with or more often without ostioles which when present appear as a dark spot or cluster of spots more or less in the centre of the surface of the conidioma, usually also opening by a single longitudinal split to one side of the conidioma, between two rows of epidermal cells; in mid-point vertical section subepidermal; in surface slice section the upper wall is absent, or so poorly developed as to be limited to a small region around any ostiole, and sometimes to a region around the split, accounting for the darker margin. *Conidiogenous cells* 5-10 $\times$ 2-4μm. *Conidia* rod shaped, 4·5-6·25 $\times$ 1μm. *Zone lines* absent or black, rare.

Typification On needles of *Pinus excelsa*, Murree, West Pakistan, Aug. 1948, No. 2594 and Aug. 1949, No. 3010.

Petrak & Ahmad (1954) in the original description, cited the two specimens above as types, but indicated no preference. The numbers cited for each specimen are Ahmad's accession numbers. The locality of these specimens is not known, but if found, a lectotype should be chosen from them.

Selected specimens examined: On *P. excelsa*, Chakar, Muzaffarabad, West Pakistan, 19 July 1963, S. Ahmad, IMI 226109a; also IMI 87030a, 139767, 139876, 162216, 177093, 177124, 197396, 231775, 235067, 236760, 247582b, 247583, 247584, 247585, 247586b, 247587, 247594, 247596, 247597, 247598.

Hosts: *Pinus ayacahuite*[0], *P. banksiana*[0], *P. cembra*[0], *P. excelsa*, *P. kesiya*, *P. koraiensis*, *P. longifolia*, *P. parviflora*, *P. patula*, *P. pentaphylla*, *P. peuce*, *P. pumila*, *P. strobus*[0], *P. taeda*[0], *P. wallichiana*.

Distribution: Asia: India, Japan, West Pakistan. Europe: Belgium[0], Great Britain[0], Ireland[0]. North America: Canada (Ontario[0]).

Cultures: Indistinguishable from cultures of *L. pinastri*.

Fruiting period: No information.

Ecology: In England, *L. pini-excelsae* has been observed fruiting on senesced needles in the litter (habitat category 1) of *P. pumila*, an introduced tree. There is no information on the ecology of *L. pini-excelsae* in regions where it is indigenous.

Notes: In the past *L. pini-excelsae* has been confused with *L. staleyi*, a similar species. They differ in hosts, *L. pini-excelsae* occurring predominantly on haploxylon, and *L. staleyi* on diploxylon pines, in characteristics of the conidiomata, *L. pini-excelsae* conidiomata virtually lacking an upper wall, and in conidium lengths.

Literature: None.

13. Lophodermium pini-pumilae Sawada, *Bulletin of the Government Forest Experimental Station Tokyo* **53**: 151, 1952. (Figs. 13, 29, 63, 64, 65)

Diagnostic features: Ascocarps black with a grey surround and black or brownish perimeter line, totally subepidermal, lips probably absent;

conidiomata subepidermal, upper wall very poorly developed, ostioles in the centre of the surface; zone lines absent or black, infrequent.

Ascocarps on secondary needles, on the abaxial side, when wet shiny and black, when dry black in the centre for more than half the total surface area, with a grey surround and a black or brownish perimeter line making a clearly marked outline, elliptical, not or only slightly raising the surface of the needle, 900-1200μm long (perimeter line), opening by a single longitudinal split, lips probably absent; in mid-point vertical section totally subepidermal, the clypeus becoming paler on either side and not extending as far as the basal wall which is very poorly developed, being present only at the perimeter of the ascocarp; in surface slice section aliform tissue is present in the clypeus. *Paraphyses*, *asci* and *ascospores* not mature in the specimen examined. *Paraphyses* swollen or unswollen at the apex (fide Sawada). *Asci* 67-104 $\times$ 7-11μm (fide Sawada). *Ascospores* 87-91 $\times$ 2μm (fide Sawada).

Conidiomata on secondary needles, on the abaxial side, the same colour as, or slightly paler than the needle, sometimes with a darker margin, elliptical to elongated elliptical, not or only slightly raising the needle surface, smooth, coalescing infrequently, 150-350μm long, with or without ostioles which when present appear as a dark spot or cluster of spots more or less in the centre of the conidioma, sometimes also opening by a single longitudinal split to one side of the conidioma, between two rows of epidermal cells; in mid-point vertical section subepidermal; in surface slice section the upper wall is absent, or so poorly developed as to be limited to a small region around any ostiole, and sometimes to a region around the split, accounting for the darker margin. *Conidiogenous cells* 5-10 $\times$ 2-4μm. *Conidia* 4·5-6·5 $\times$ 1μm. *Zones lines* absent or black, infrequent.

Typification: On needles of *Pinus pumila*, Honshu, Japan. The locality of this specimen is not known.

Specimen examined: On *P. pumila*, Furano, Hokkaido, Japan, 17 June 1975, Takahashi, IMI 247563a.

Hosts: *Pinus pumila*.

Distribution: Asia: Japan.

Cultures: No information.

Fruiting period: No information.

Ecology: No information.

Notes: The fungus observed on the specimen cited above is tentatively associated with the name *L. pini-pumilae*. *Lophodermium pini-pumilae* differs from *L. pini-excelsae* in being totally subepidermal, with a very poorly developed basal wall and probably no lips (the specimen examined is immature). *Lophodermium pini-excelsae* is rarely totally subepidermal, and the basal wall is always more developed and visible in vertical sections right across the base of the ascocarp. *Lophodermium pini-pumilae* differs from *L. orientale* in external appearance of the ascocarps, and in having a more developed clypeus and at least some basal wall present.

Literature: None.

14. Lophodermium orientale Minter sp. nov. (Figs. 14, 30, 63, 64, 65)

Diagnostic features: Ascocarps inconspicuous, grey without a perimeter line, totally subepidermal, lips absent; conidiomata absent; zone lines absent.

Ascocarps on secondary needles, on all sides, when wet black and shiny, when dry grey for a small region around the split, with no perimeter line and so with a poorly marked outline, elliptical, raising the surface of the needle, 350-850μm long (clypeus extent), opening by a single longitudinal split, lips absent; in mid-point vertical section totally subepidermal, the clypeus being poorly developed and becoming paler on either side, the basal wall being absent; in surface slice section aliform tissue is absent from the clypeus. *Paraphyses* tips straight and unswollen. *Asci* 60-95 $\times$ 9-12μm. *Ascospores* 55-85 $\times$ 2μm. *Conidiomata* and *zone lines* absent.

Ab aliis *Lophodermii* speciebus quae in *Pini* acubus ascocarpos subepidermales producant differt quod neque murum inferiorem neque labia habet.

Typification: On needles of *Pinus excelsa*, Doonga Gali, West Pakistan, 16, Aug. 1975, Ahmad, Fungi of West Pakistan 24830, IMI 197396b, holotype.

Specimens examined: On *P. excelsa*, Doonga Gali, West Pakistan, 16 Aug. 1975, Ahmad, IMI 197396b, holotype; also IMI 139876b, 226109b.

Hosts: *Pinus excelsa.*

Distribution: West Pakistan.

Cultures: No information.

Fruiting period: No information.

Ecology: No information.

Notes: *Leptostroma*-like conidiomata occur on the same needles as ascocarps of this species, but it is not clear if they are connected with *L. orientale.*

Literature: None.

15. Lophodermium canberrianum Stahl ex Minter & Millar, *Transactions of the British Mycological Society* **71**: 336-337, 1978. (Figs. 15, 31, 63, 64, 65, Plate 1d, j)

Diagnostic features: Ascocarps grey, without a perimeter line, the pine epidermis being often a tawny colour around the split, totally subepidermal, lips present; conidiomata absent; zone lines absent.

Ascocarps on secondary needles, on all sides (< 40% on adaxial or radial sides), when wet black or grey, when dry grey, the needle epidermis being often a tawny colour around the split, with no perimeter line and so with a poorly marked outline, elliptical, raising the surface of the needle, 600-1400μm long (clypeus extent), opening by a single longitudinal split, lips present, colourless; in mid-point vertical section totally subepidermal,

the clypeus becoming paler on either side, the basal wall being absent; in surface slice section aliform tissue is present in the clypeus but is poorly developed. *Paraphyses* tips slightly swollen, rarely branched. *Asci* 110-150 × 11-15μm. *Ascospores* 70-120 × 2μm. *Conidiomata* absent. *Zone lines* absent.

Typification: On needles of *Pinus engelmannii*, Blundel's Farm Arboretum, Australian Capital Territory, Australia, 18 Dec. 1976, W. Stahl, IMI 223611, holotype.

Specimens examined: On *P. engelmannii*, Blundel's Farm Arboretum, Australian Capital Territory, Australia, 18 Dec. 1976, W. Stahl, IMI 223611, holotype; also IMI 213003, 225310, 247601.

Hosts: *Pinus engelmannii*, *P. ponderosa*.

Distribution: Australasia: Australia (Australian Capital Territory⁰, Victoria⁰).

Cultures: Slow growing, fluffy, white later becoming orange or yellow, growth always ceasing before the edge of the dish is reached, never developing zone lines on the circumference, conidia not observed.

Fruiting period: All year round, but mainly in the winter (fide Stahl).

Ecology: In Australia *L. canberrianum* is more tolerant than *L. pinastri* of dry conditions, and is observed only on *P. ponderosa* and its closest relatives, sometimes causing severe defoliation (fide Stahl).

Notes: *Lophodermium canberrianum* is similar to *L. orientale*, but has ascocarps with lips, and lacks conidiomata. Pines of the *ponderosa* group are not native to Australia, and it is surprising therefore to see *L. canberrianum* occurring on their needles in Australia, but not, apparently, in North America where these trees are native. Either *L. canberrianum* is present but as yet undiscovered in North America, or perhaps it is a fungus native to Australia which has recently adopted pines of the *ponderosa* group as new hosts. The answer to this problem might well clarify recent speculation on the evolution of *Lophodermium* and its related genera (Pirozynski & Weresub, 1979).

Literature: Minter & Millar (1978a, 1978b), Stahl (1966).

16. Lophodermium durilabrum Darker, *Contributions from the Arnold Arboretum of Harvard University* **1**: 87-88, 1932. (Figs. 16, 32, 63, 64, 65, Plate 1e, f)

Diagnostic features: Ascocarps black to dark grey, with a paler brownish central band and a perimeter line, centrally subhypodermal, lips absent; conidiomata absent; zone lines absent.

Ascocarps on secondary needles, on the abaxial side, when wet black, when dry black to dark grey, with a paler brownish central band and a perimeter line making a more or less well defined margin, elliptical, raising the surface of the needle slightly, 880-1750μm long (perimeter line), opening by a single longitudinal split, lips absent; in mid-point vertical section centrally subhypodermal, the clypeus extending on either side to the

edge of the ascocarp, the basal wall being poorly developed and sometimes visible only in the centre; in surface slice section aliform tissue is absent. *Paraphyses* tips straight and not or only slightly swollen. *Asci* 110-130 × 8-9μm. *Ascospores* 90-105 × 2μm. *Conidiomata* absent. *Zone lines* absent.

Typification: On needles of *Pinus monticola*, Horsethief Meadows, Hood River County, Oregon, United States, 6 July 1929, L. N. Goodding & G. D. Darker, Arnold Arboretum Pathological Herbarium 157, holotype. Now in FH.
Specimen examined: On *P. monticola*, Horsethief Meadows, Hood River County, Oregon, United States, 6 July 1929, L. N. Goodding & G. D. Darker, FH, holotype.
Hosts: *Pinus aristata*, *P. monticola*, *P. strobus*.
Distribution: North America: United States (California, Oregon, Wisconsin).
Cultures: No information.
Fruiting period: No information.
Ecology: Weakly parasitic (fide Darker).
Notes: The black zone lines reported by Tehon (1935) for *L. durilabrum* arise from a misinterpretation of the type specimen on which *L. nitens* is also present.
Literature: Anon. (1969), Darker (1932[b], 1967), Greene (1949), Miller (1969), Tehon (1935).

17. Pseudostypella translucens (Gordon) Reid & Minter, *Transactions of the British Mycological Society* **72**: 347, 1979. (Figs. 57, 58, 59)
≡ *Tremella translucens Gordon* (1938).
Diagnostic features: Basidiocarps parasitizing ascocarps of species of *Lophodermium* and *Meloderma* Darker, inconspicuous when dry, expanded, conspicuous, white and gelatinous, bursting out of the ascocarp when wet.

Basidiocarps appearing as if erumpent from secondary needles, but in reality emerging from the deformed split of parasitized ascocarps of species of *Lophodermium* and *Meloderma*, contracted, inconspicuous, brown and horny when dry, expanded up to 2mm diameter, conspicuous, white and gelatinous when wet, and cushion shaped with a smooth dimpled or somewhat irregularly wrinkled surface, making the ascocarps more round than normal and opening with splits not lined with the usual lips; in mid-point vertical section the clypeus and basal wall are all that remain of the ascocarp, the basidiocarp context being gelatinous, formed of dense, thin-walled hyaline hyphae, 1·7-3·3μm wide with clamp connections at the septa, the hyphae showing characteristic swelling on the side of the septum away from the clamp, the hymenium being a zone about 40μm deep of densely crowded basidia which originate at all levels. *Basidia* more or less globose, with a basal clamp connection, cross-septate,

10-13 × 9·5-10μm, bearing four basidiospores. *Basidiospores* elliptical to slightly allantoid, hyaline, aseptate, 7-9 × 3-4μm.

Typification: On needles of *Pinus sylvestris*, emerging from *Lophodermium conigenum*, Glentress Forest, Peebles, Scotland, 7 Aug. 1936, holotype, E.

Selected specimens examined: Emerging from *Lophodermium conigenum*: on *P. sylvestris*, Glentress Forest, Peebles, Scotland, 7 Aug. 1936, holotype, E, also isotype, K; on *P. sylvestris*, Teintsmuir, Fife, Scotland, April 1978, B. L. K. Brady, K; on *P. sylvestris*, Kingswells, Aberdeen, Scotland, 3 Nov. 1976, D. W. Minter, K; on *P. sylvestris*, Culbin Forest, Morayshire, Scotland, 23 Mar. 1977, D. W. Minter, K; on *P. sylvestris*, Tarland, Aberdeenshire, Scotland, 30 Sept. 1977, D. W. Minter, K; on *P. banksiana*, Thunder Bay, Ontario, Canada, 17 June 1963, R. F. Cain, K. Emerging from *Lophodermium pinastri*: on *P. mugo*, Taschcach, Austria, 15 Sept. 1977, C. S. Millar, K. Emerging from *Lophodermium seditiosum*: on *P. sylvestris*, Kinloch, Rhum, Hebrides, Scotland, 28 & 29 Aug. 1962, R. W. G. Dennis, K; on *P. sylvestris*, Papadil, Rhum, Hebrides, Scotland, June 1977, A. P. Bennell, K. Emerging from *Lophodermium* sp.: on *P. resinosa*, Haney, British Columbia, Canada, 5 May 1964, D. H. Ruppel, K. Emerging from *Meloderma desmazieresii* (Duby) Darker: on *P. strobus*, Banja Luka, Yugoslavia, 19 Sept. 1977, V. Lazarev & C. S. Millar, K.

Hosts: *Lophodermium conigenum* on *Pinus banksiana*, *P. densiflora*[0], *P. mugo*, *P. nigra* var. *maritima*, *P. sylvestris*, *P. tabuliformis*[0]; *Lophodermium pinastri* on *P. mugo*; *Lophodermium seditiosum* on *P. sylvestris*; *Lophodermium* sp. on *P. resinosa*; *Meloderma desmazieresii* on *P. strobus*.

Distribution: Europe: Austria, Great Britain, Yugoslavia. North America: Canada (British Columbia, Ontario).

Cultures: No information.

Fruiting period: In Scotland on secondary needles of *P. sylvestris*, *Pseudostypella translucens* appears on ascocarps of *Lophodermium conigenum* shortly after they open, and remains visible for at least ten months, probably longer.

Ecology: *Pseudostypella translucens* is known only from ascocarps of *Lophodermium* and *Meloderma* on pine needles and cones. It seems to be an obligate parasite of these fungi and its ecology is therefore closely related to that of its hosts.

Notes: The basidiospores are easily missed, but the basidia with their cross-septa are characteristic. The fungus is most easily collected after rain, when the basidiocarps are swollen and conspicuous.

Literature: Reid & Minter (1979).

18. Cladosporium lophodermii Georgescu & Tutunaru. *Studii şi Cercetări de Biologie, Seria Biologie Vegetală* **10:** 25, 1958. (Figs. 60, 61, 62)

Diagnostic features: Brown septate hyphae ramifying throughout the hymenium of ascocarps of *Lophodermium* species.

Mycelium brown, septate, ramifying throughout the hymenium of asocarps of *Lophodermium* species. *Conidiophores* rising above the hymenium from the mycelium, erect, irregularly curved and geniculate, yellow-brown, with few septa, 110-130 × 4-5μm, the apical cell being 30-40μm long and more or less clavate at the tip. *Conidia* variable in shape, irregularly ellipsoid or ovoid, brown, smooth or slightly warted, often rounded at the apex, often aseptate 5-15 × 5-6μm, 1 septate 10-18 × 5-8μm, or rarely 2 septate 18-21 × 5·5μm or 3 septate 20-26 × 5·5-6μm, but not constricted at the septa (all fide Georgescu & Tutunaru (1958)).

Typification: On needles of *Pinus sylvestris*, emerging from *Lophodermium pinastri*, Oraşul Stalin, Romania, June 1956. The locality of this specimen is not known, but may be BUCA.

Specimens examined: Emerging from *Lophodermium indianum*: on *P. caribaea*, India, June 1977, S. Singh, IMI 247570a. Emerging from *Lophodermium pini-excelsae*: on *P. patula*, N. Bengal, India, July 1979, S. Singh, IMI 247586a; on *P. taeda*, N. Bengal, India, July 1979, S. Singh, IMI 247582a. Emerging from *Lophodermium* sp.: on *P. taeda*, N. Bengal, India, July 1979, S. Singh, IMI 247565a.

Hosts: *Lophodermium indianum* on *P. caribaea*[0]; *Lophodermium pini-excelsae* on *P. patula*, *P. taeda*[0]; *Lophodermium* sp. possibly *pinastri* on *P. sylvestris*; *Lophodermium* sp. on *P. taeda*[0].

Distribution: Asia: India. Europe: Romania.

Cultures: No information.

Fruiting period: No information.

Ecology: No information.

Notes: Attempts to borrow the type material have not been successful. The identification of *C. lophodermii* in the specimens examined is only tentative, the more so because no spores have been seen. Brown hyphae in immature and recently opened ascocarps of *Lophodermium* are, however, such an unusual sight that it seems reasonable tentatively to attribute them to this species. Without examining type material, it is not possible to say on the basis of the original description and illustration of *C. lophodermii* whether it is correctly placed in the genus *Cladosporium* Link ex Fr. It does appear to be different from *Cladosporium herbarum* (Pers.) Link ex S. F. Gray, which has been observed growing saprophytically on old ascocarps of *Lophodermium pinastri* (Mitchell et al., 1978).

Literature: Georgescu & Tutunaru (1958).

Doubtful or excluded species

Lophodermium amplum (Davis) Davis, *Trans. Wis. Acad. Sci. Arts Lett.* **19**: 695, 1919.

≡ *Lophodermium pinastri* var. *amplum* Davis (1918).

Darker (1967) redisposed this taxon as *Davisomycella ampla* (Davis) Darker.

Lophodermium brachysporum Rostrup, *Tidsskr. Skogbr.* **6**: 281, 1883.

A synonym of *Meloderma desmazieresii* (Duby) Darker, fide Darker (1967).

Lophodermium gilvum Rostrup, *Tidsskr. Skogbr.* **6**: 283, 1883.

A synonym of *Naemacyclus niveus* (Pers. ex Fr.) Sacc., fide Darker (1932).

Lophodermium lineare (Pk) Ellis & Everh., *N. Am. Pyren.* 721, 1892.

An obligate synonym of *Bifusella linearis* (Pk) Höhn.

Lophodermium lineatum Smith & Ramsbottom, *Trans. Br. mycol. Soc.* **6**: 365, 1920.

A synonym of *Meloderma desmazieresii* (Duby) Darker, fide Darker (1967).

Lophodermium ponderosae Staley, *Mycologia* **56**: 757, 1964.

Dubin & Staley (1969) redisposed this taxon as *Davisomycella ponderosae* (Staley) Dubin.

Leptostroma ahmadii Petr. & Ahmad, *Sydowia* **8**: 181, 1954.

A synonym of *Hypodermium effusum* Schw., fide Minter (1980a).

Leptostroma confluens Cooke, *Grevillea* **12**: 22, 1883.

This species was described from a specimen on bark of pine, and appears to be neither a good *Leptostroma* nor an anamorph of *Lophodermium*.

Leptostroma hedgcockii Dearness, *Mycologia* **18**: 240, 1926.

A fungus of doubtful affinities, clearly not a *Leptostroma*, fide Minter (1980a).

Leptostroma pinastri Desm., *Annls Sci. nat.* II. **19**: 338, 1843.

An earlier name for *Sirothyriella pini-austriacae* (Roum. & Fautr.) Sutton, fide Minter (1980a). The formal new combination is made below.

Sirothyriella pinastri (Desm.) Minter comb. nov.

Basionym: *Leptostroma pinastri* Desm., *Annls Sci. nat.* II. **19**: 338, 1843.

=*Sirothyriella pini-austriacae* (Roum. & Fautr.) Sutton (1977).

Leptostroma strobicola Hilitz., *Věd. Spisy Česk. Akad. Zeměd.* **3**: 149, 1929.

The anamorph of *Meloderma desmazieresii* (Duby) Darker.

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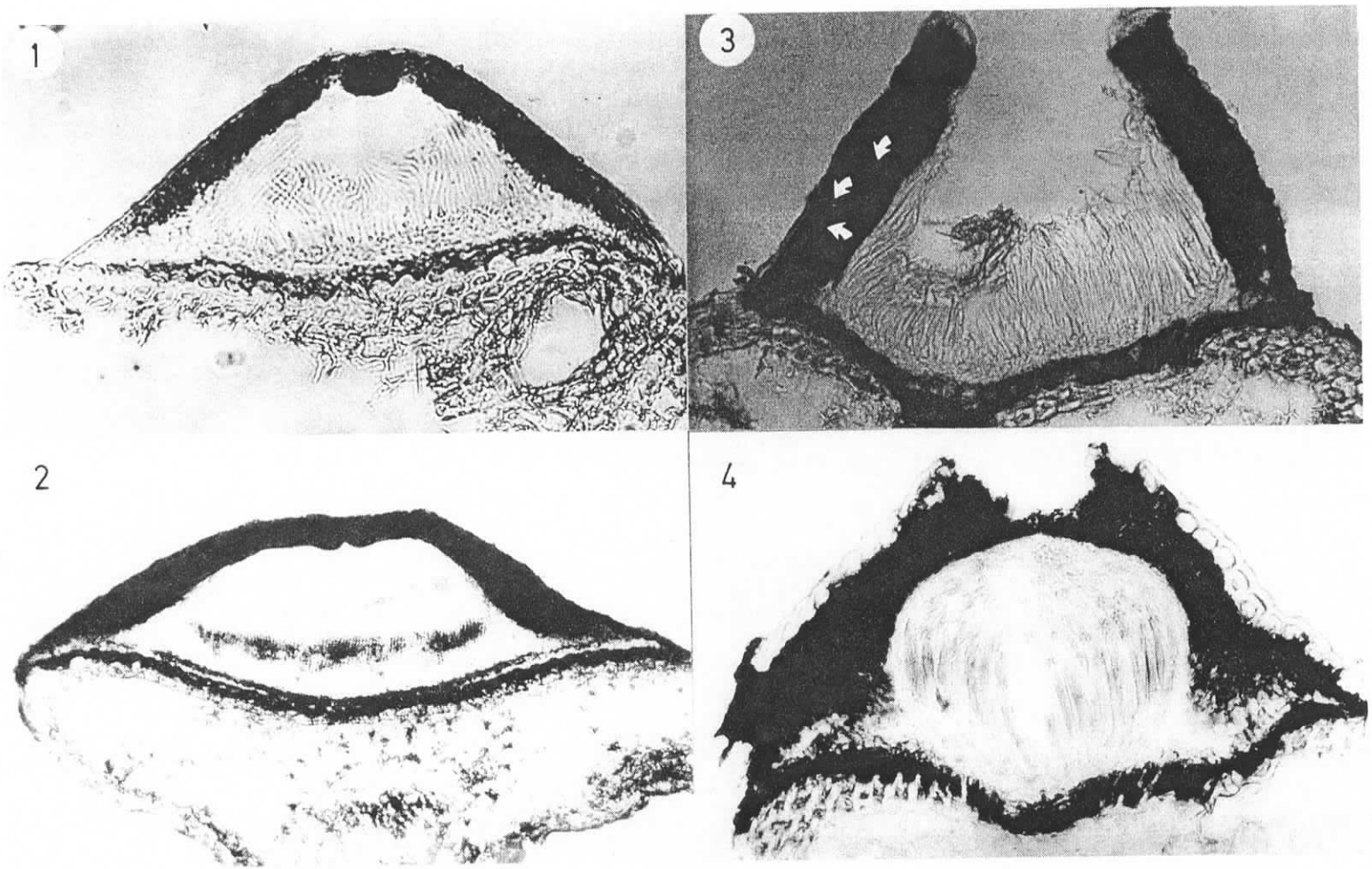
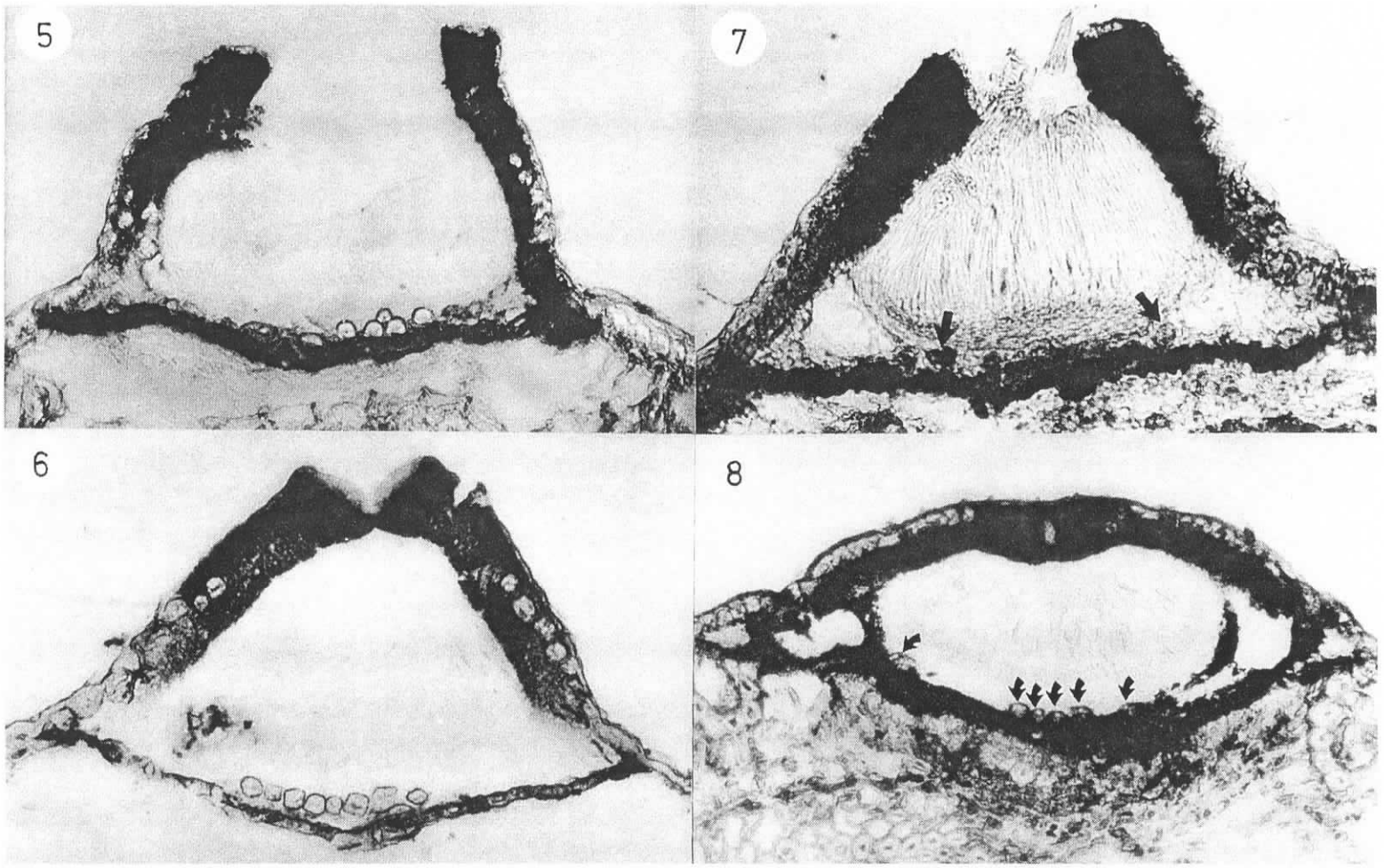
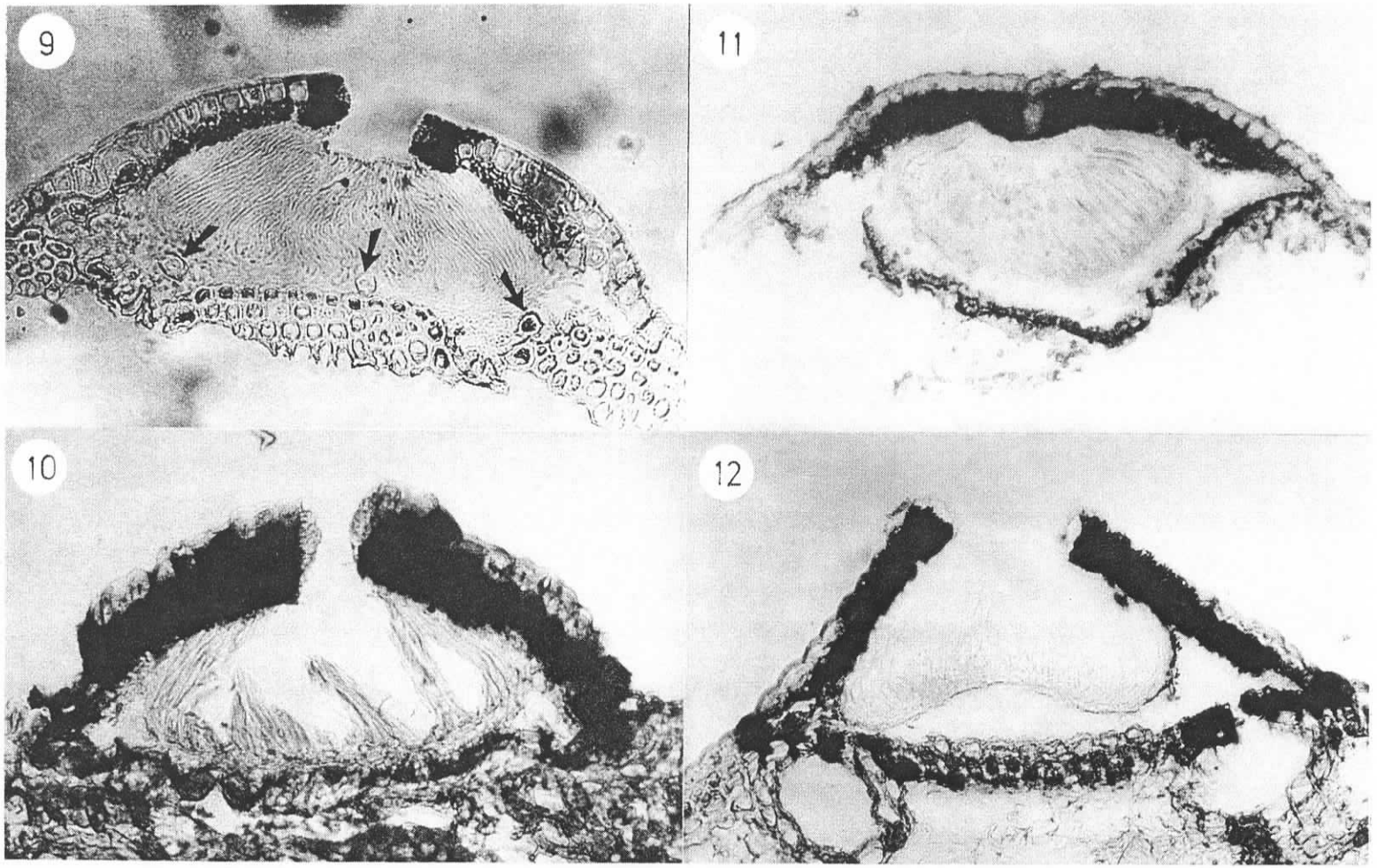
FIGURES



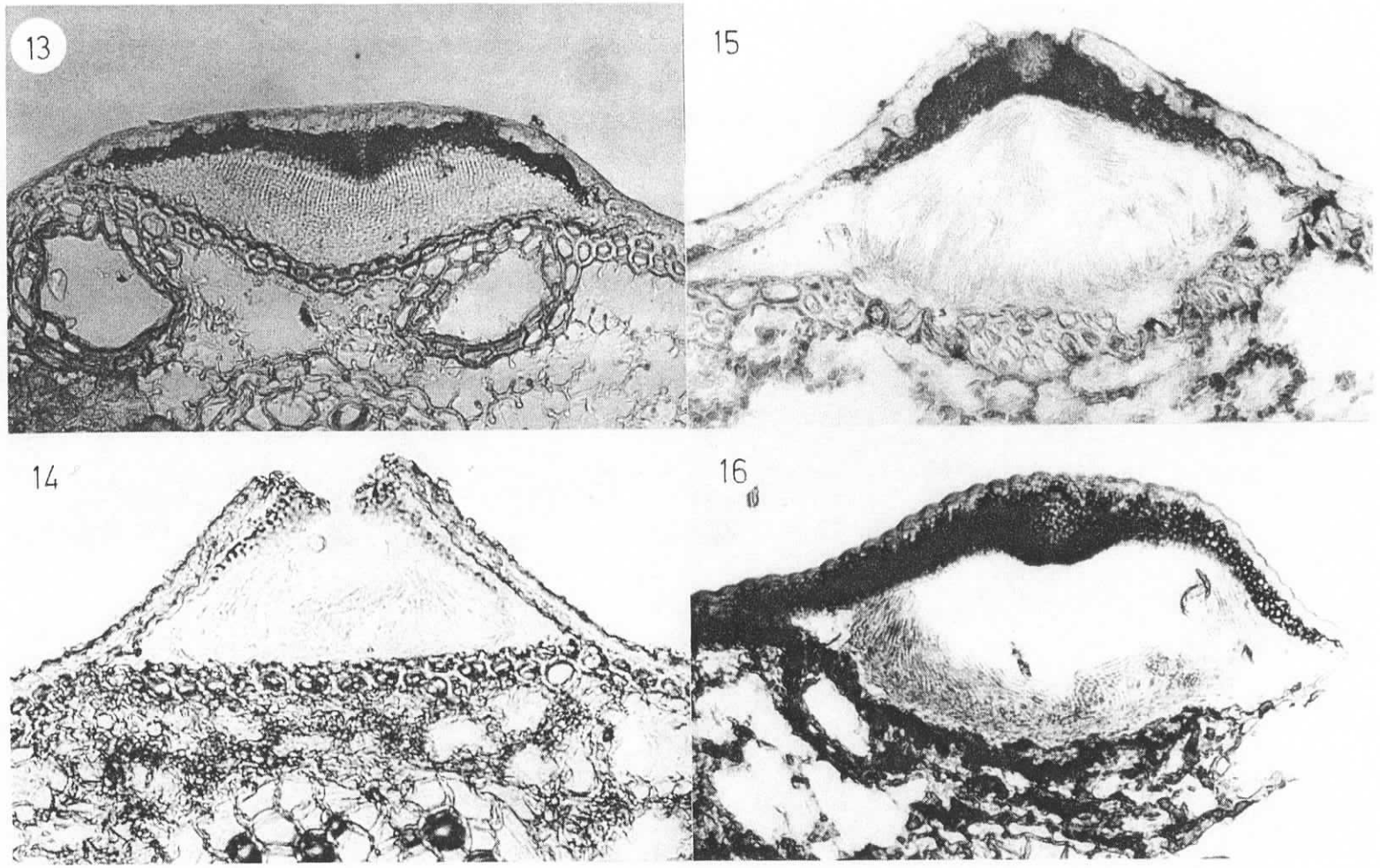
FIGS 1-4. Ascocarps of *Lophodermium* species in vertical section: 1 *L. nitens* (× 120), 2 *L. sp.* (× 120), 3 *L. molitoris* (× 100) arrows point to some of the epidermal cells embedded in the clypeus, 4 *L. baculiferum* (× 110).



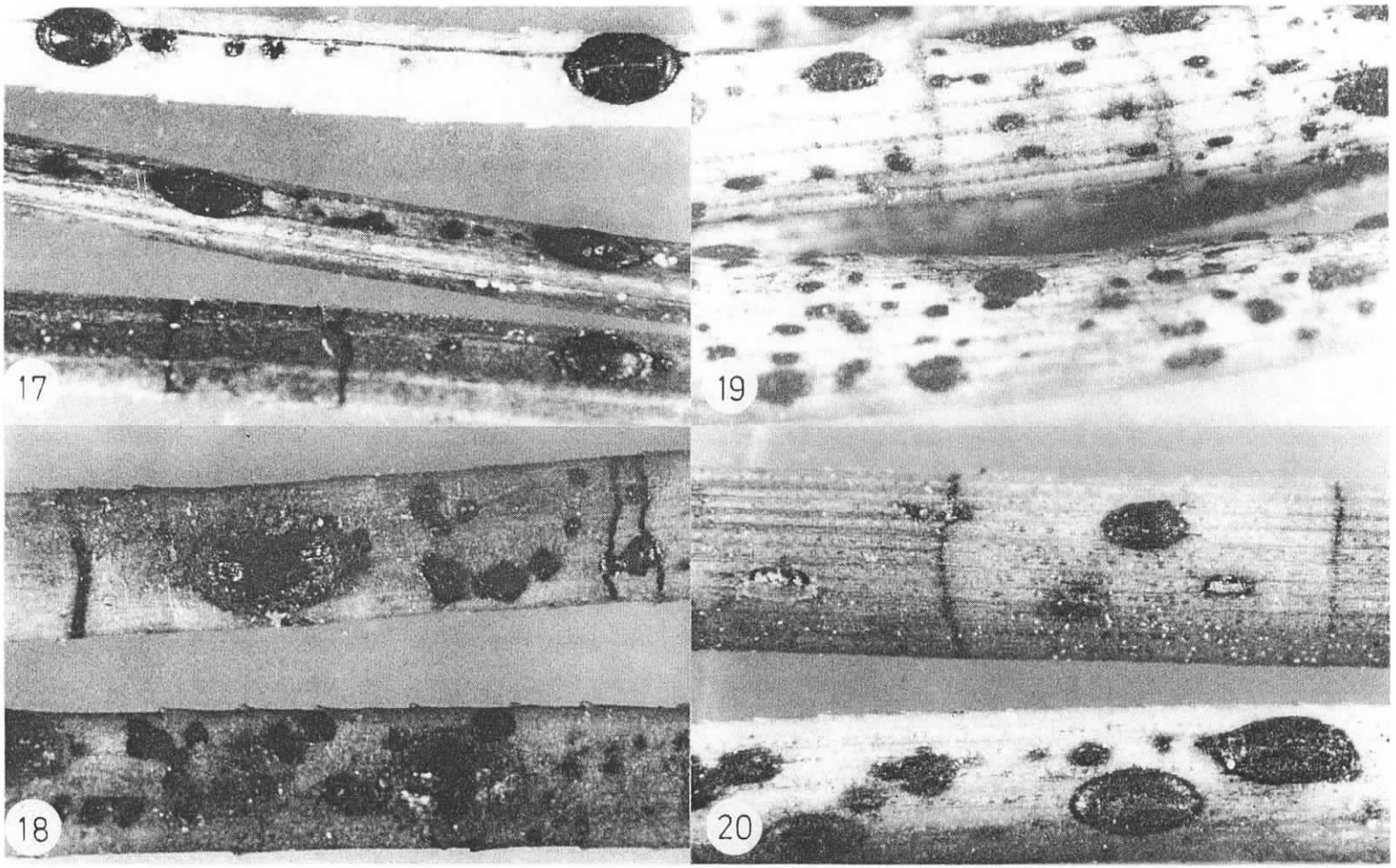
FIGS 5-8. Ascocarps of *Lophodermium* species in vertical section: 5 *L. staleyi* (× 150), 6 *L. pinastri* (× 100), 7 *L. indianum* (× 130) arrows point to epidermal cells dispersed on ascocarp floor, 8 *L. conigenum* (× 100) arrows point to epidermal cells dispersed on ascocarp floor.



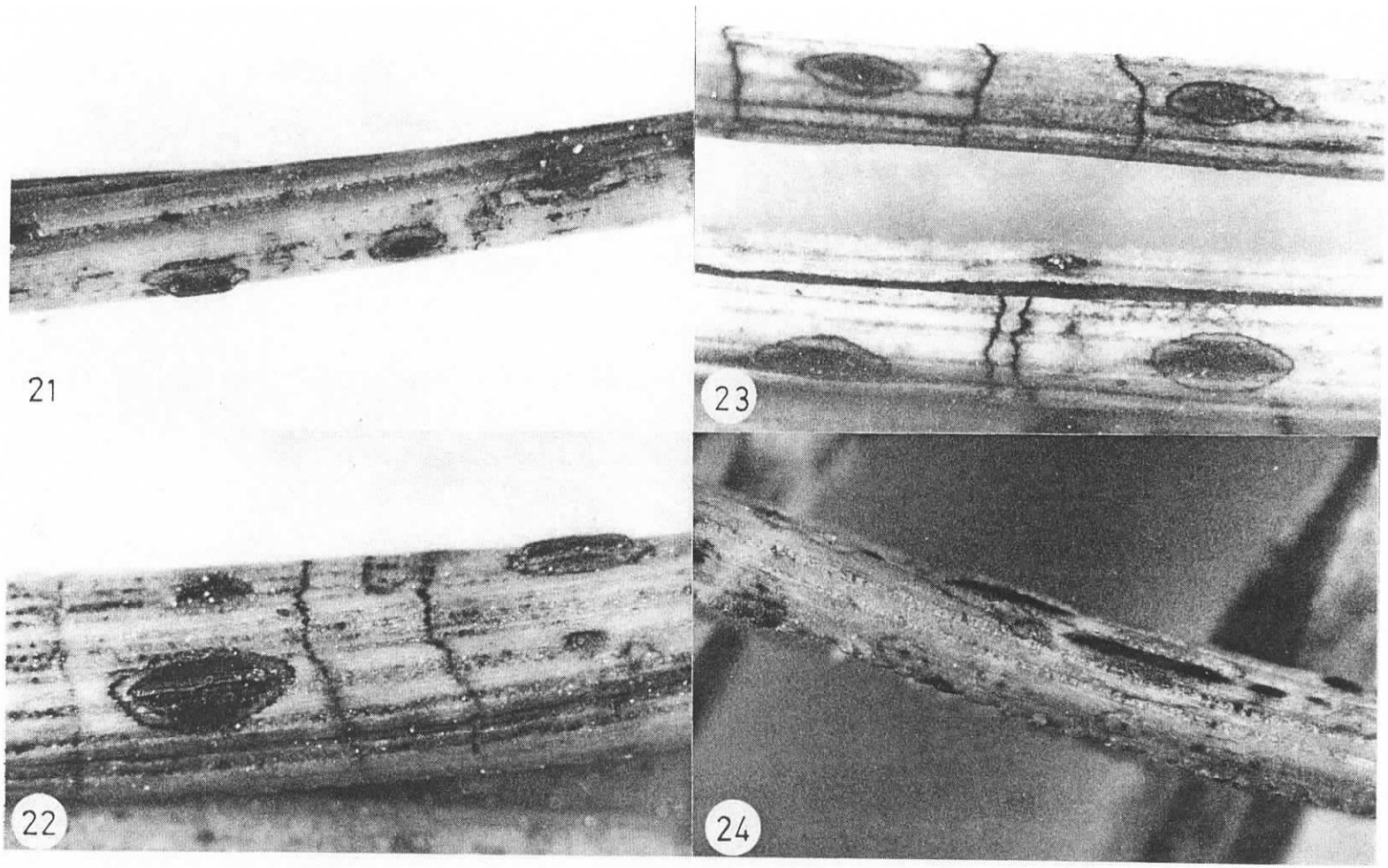
FIGS 9-12. Ascocarps of *Lophodermium* species in vertical section: 9 *L. australe* (× 100) arrows point to epidermal cells dispersed on ascocarp floor, 10 *L. ravenelii* (× 110), 11 *L. seditiosum* (× 100), 12 *L. pini-excelsae* (× 150).



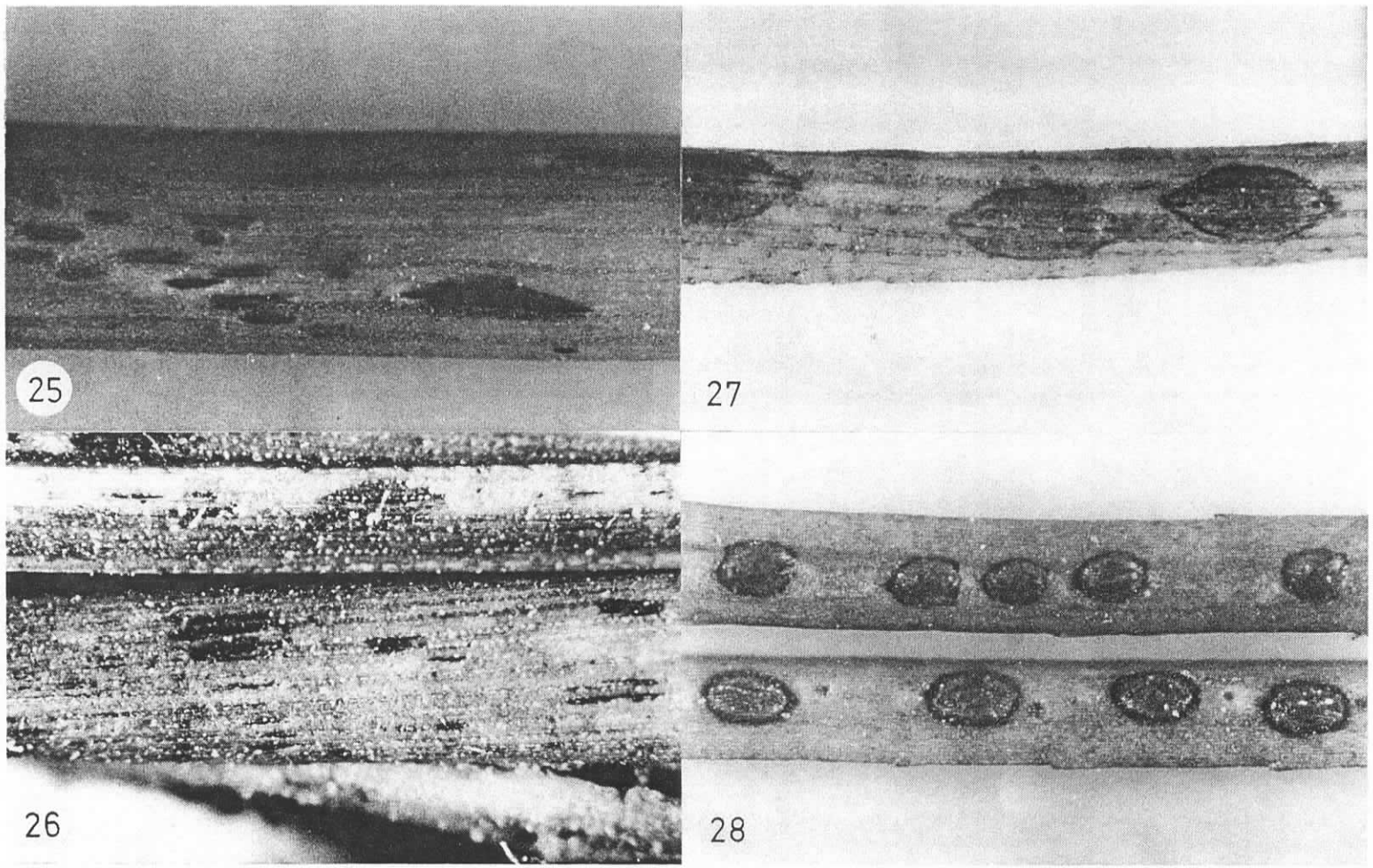
FIGS. 13-16. Ascocarps of *Lophodermium* species in vertical section: 13 *L. pini-pumilae* (× 100), 14 *L. orientale* (× 110), 15 *L. canberrianum* (× 100), 16 *L. durilabrum* (× 100) the position of hypodermal cells in this species is seen better in plate 1f.



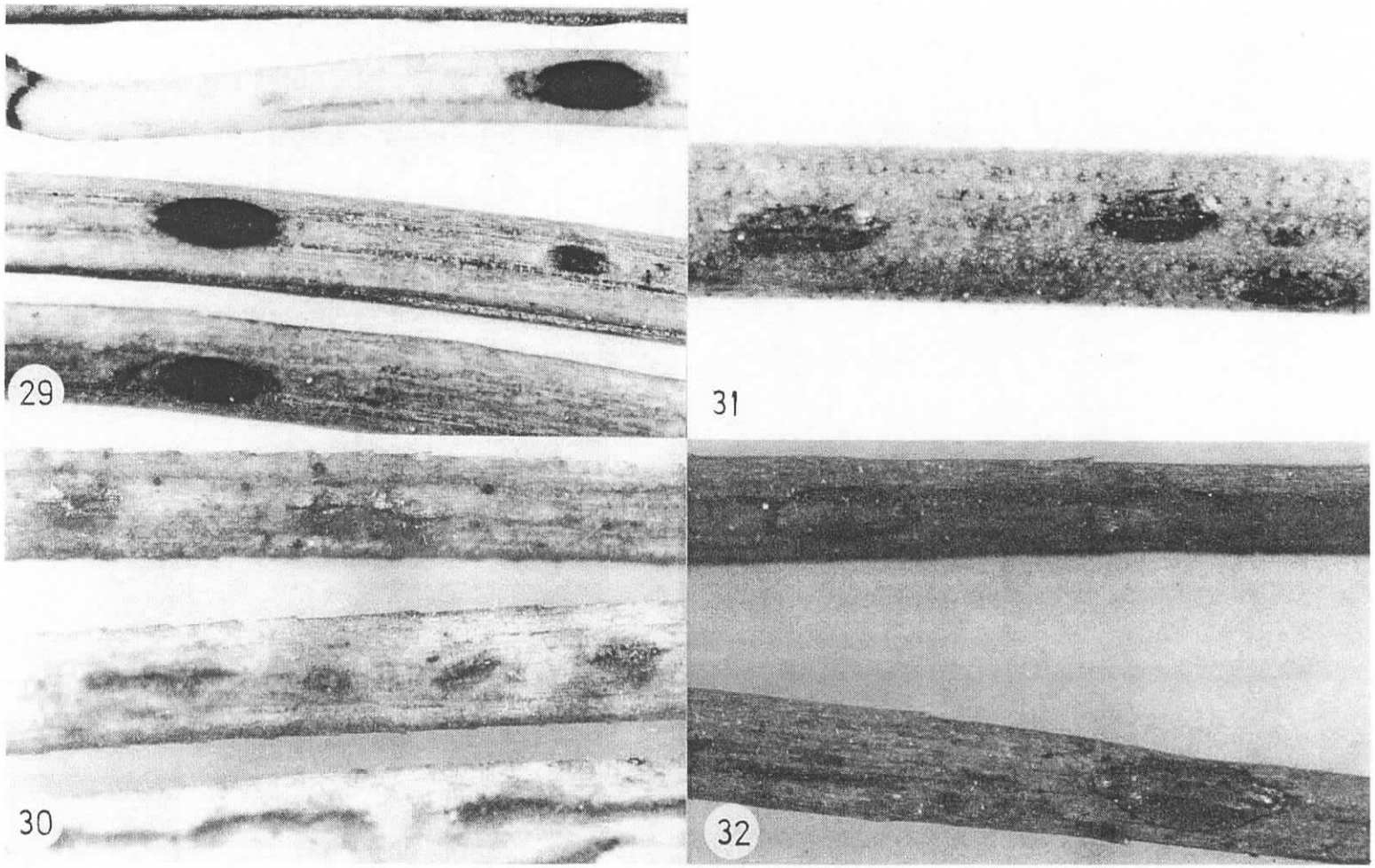
FIGS 17-20. General views of *Lophodermium species* on secondary needles: 17 *L. nitens* (× 12), 18 *L. sp.* (× 22), 19 *L. molitoris* (× 10), 20 *L. baculiferum* (× 15).



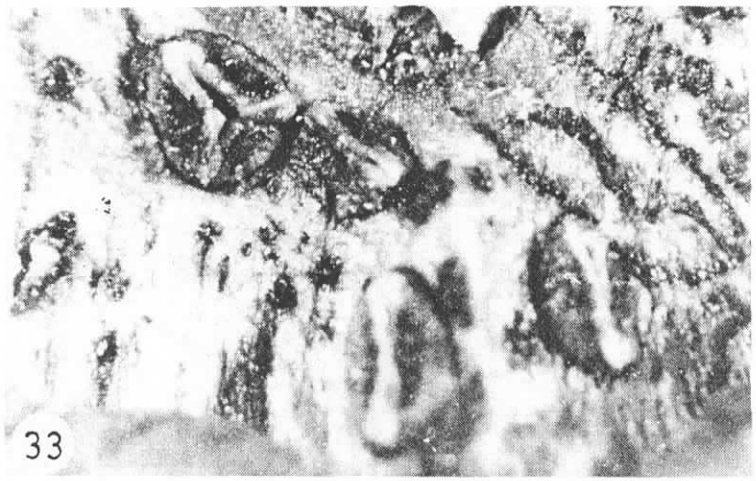
FIGS 21-24. General views of *Lophodermium* species on secondary needles: 21 *L. staleyi* (× 12), 22 *L. pinastri* (× 20), 23 *L. indianum* (× 13), 24 *L. conigenum* (× 20).

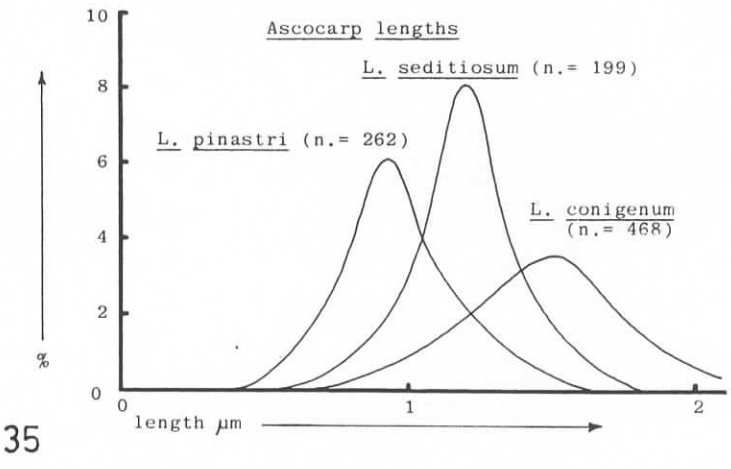


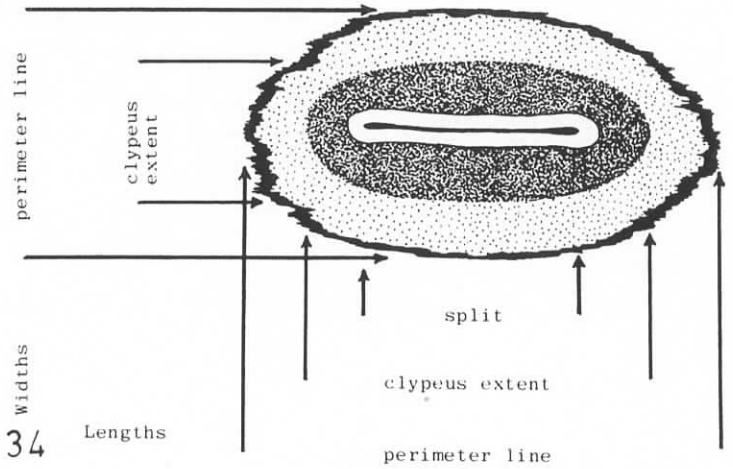
FIGS 25-28. General views of *Lophodermium* species on secondary needles: 25 *L. australe* (× 20), 26 *L. ravenelii* (× 15), 27 *L. seditiosum* (× 20), 28 *L. pini-excelsae* (× 14).



FIGS 29-32. General views of *Lophodermium* species on secondary needles: 29 *L. pini-pumilae* (× 15) these ascocarps are immature and the perimeter line is not yet visible clearly, 30 *L. orientale* (× 13) 31 *L. canberrianum* (× 15), 32 *L. durilabrum* (× 20).







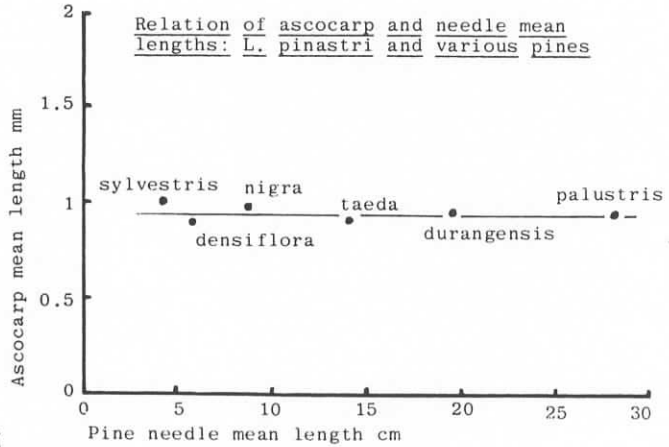


FIG 33. Ascocarps of *L. seditiosum* on a cone of *P. sylvestris*, showing both longitudinal and radial splitting (×20).
FIG. 34. Ascocarp dimensions.
FIG. 35. Histogram comparing ascocarp lengths of *L. pinastri*, *L. seditiosum* and *L. conigenum*.
FIG. 36. Relation of ascocarp and needle mean lengths: *L. pinastri* and various pines.

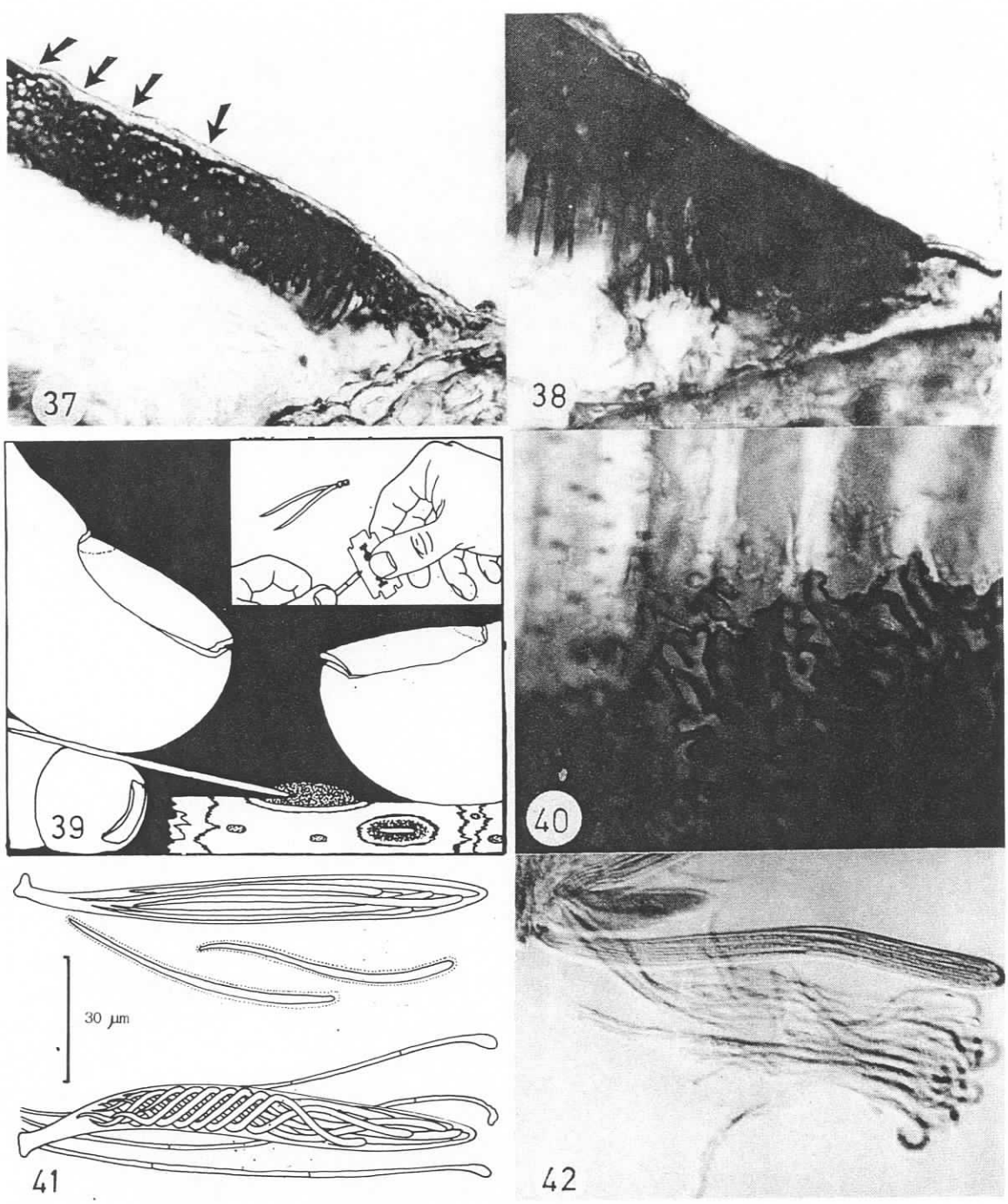


FIG. 37. Ascocarp clypeus of *L. nitens* in vertical section, showing textura angularis. (× 300) arrows point to some of the indentations in the cuticle.
FIG. 38. Ascocarp clypeus of *L. nitens* in vertical section showing textura prismatica (× 600).
FIG. 39. Cutting a surface slice section.
FIG. 40. Aliform tissue of *L. baculiferum* (× 600).
FIG. 41. Asci, ascospores and paraphyses of *L. pinastri*.
FIG. 42. Asci, ascospores and paraphyses of *L. baculiferum* (× 500).

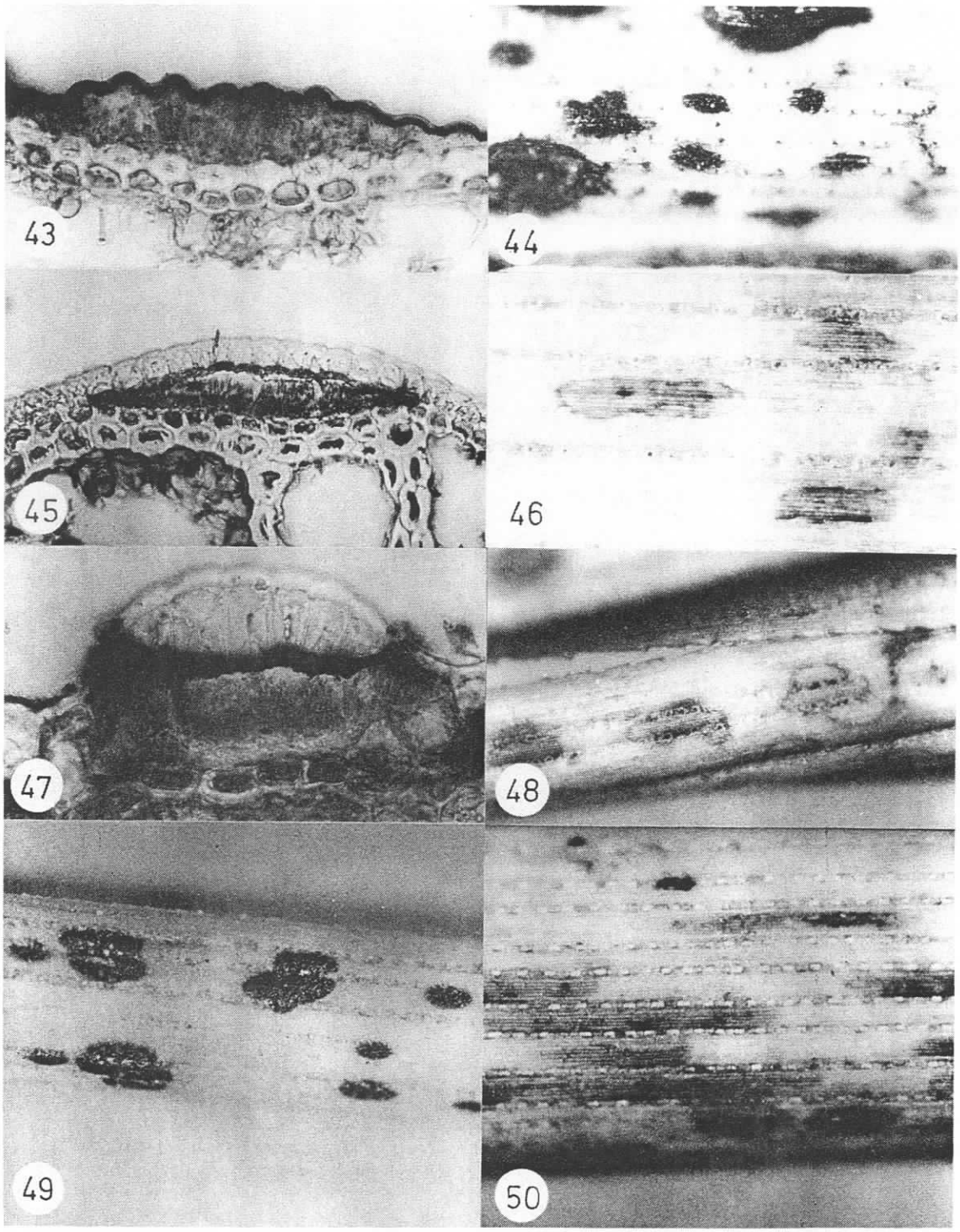
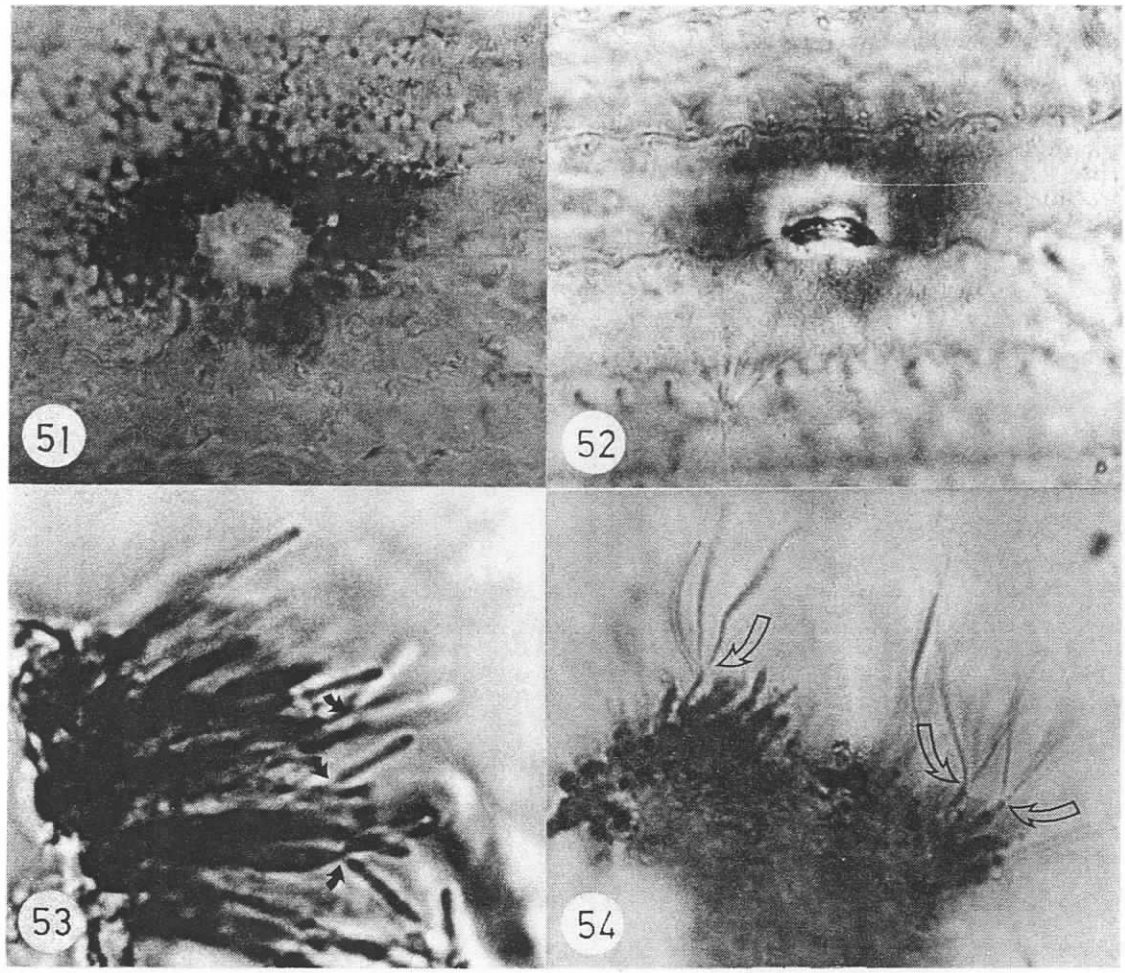
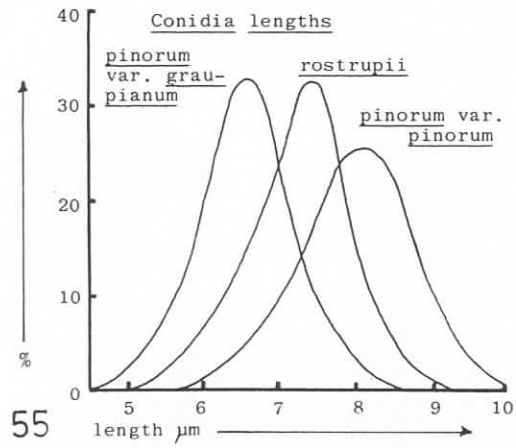


FIG. 43. Conidioma of *L. nitens* in vertical section (× 350).
FIG. 44. Conidiomata of *L. molitoris* (× 35).
FIG. 45. Conidioma of *L. conigenum* in vertical section (× 350).
FIG. 46. Conidiomata of *L. conigenum* (× 70).
FIG. 47. Conidioma of *L. pinastri* in vertical section (× 350).
FIG. 48. Conidiomata of *L. pinastri* (× 30).
FIG. 49. Conidiomata of *L baculiferum* showing lateral coalescing (× 30).
FIG. 50. Conidiomata on *L. australe* showing longitudinal coalescing (× 40).





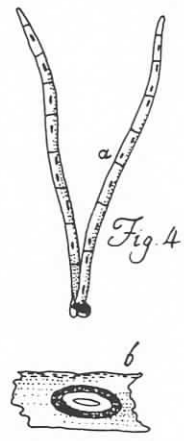


Fig. 4. Hysterium *Pinastri*.

a. folia Pin. *syluestr.* cum nonnullis indiuiduis huius Hysterii, quoad habitum naturalem.

b. vnicum indiuidium sub lente exhibitum.

Schrader: Journ. für die Botanik 1799.

56

FIG. 51. Detail of ostiole of conidioma of *L. conigenum* (× 600).
FIG. 52. As Fig. 51, but refocussed to show the split in the epidermis (× 600).
FIG. 53. Conidiogenous cells and conidia of *L. seditiosum* (× 1000), arrows point to 'rabbit's ears'.
FIG. 54. Conidiogenous cells and conidia of *L. ravenelii* (× 800), arrows point to 'rabbit's ears'.
FIG. 55. Histogram comparing conidia lengths of *Leptostroma pinorum* var. *pinorum*, *L. pinorum* var. *graupianum* and *L. rostrupii*.
FIG. 56. Copy of Schrader's original illustration of *Hysterium pinastri*.

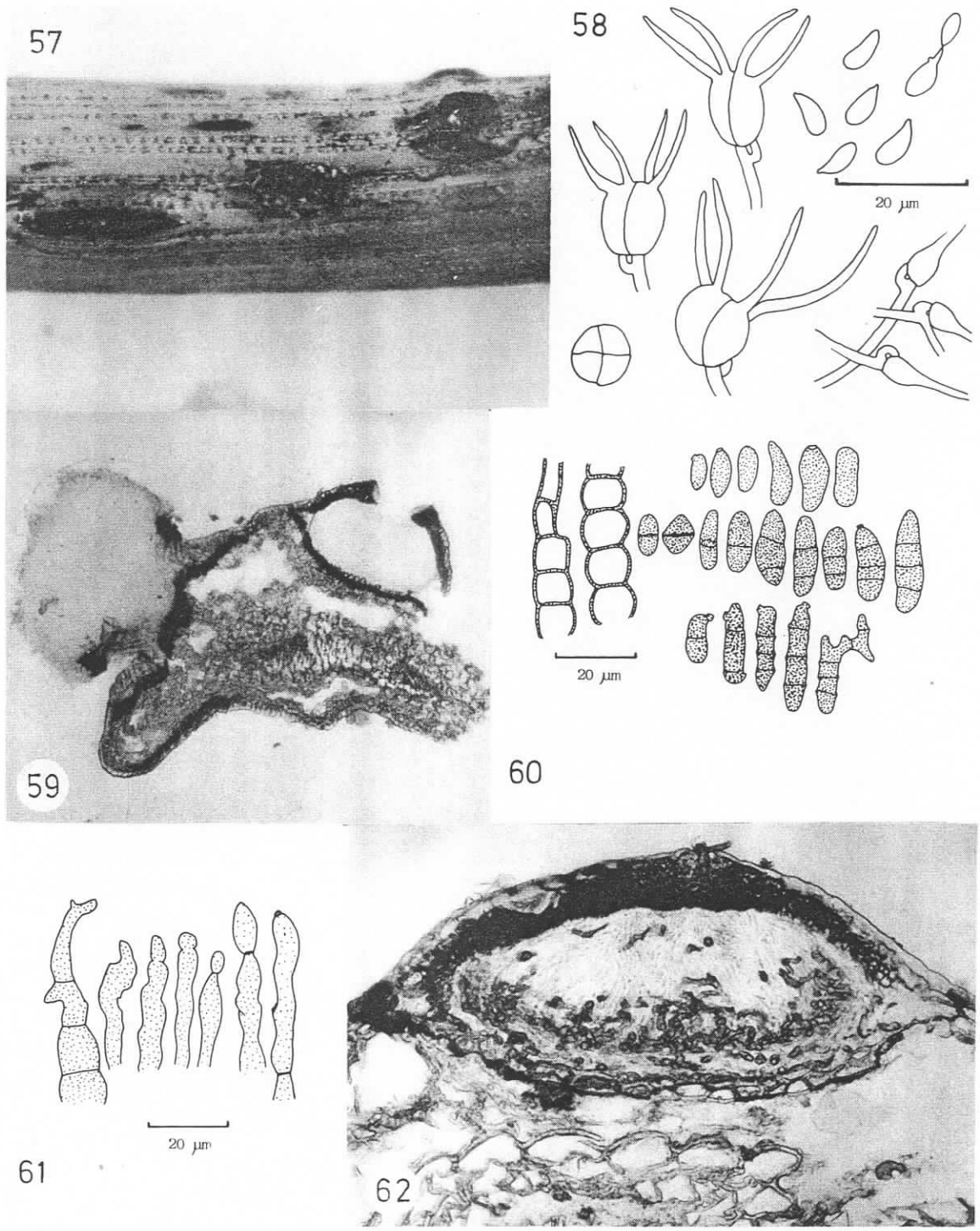


FIG. 57. Healthy and parasitised ascocarps of *L. conigenum*, with *Pseudostypella translucens* (× 20).
FIG. 58. Basidia, basidiospores and clamp connections of *P. translucens*.
FIG. 59. Vertical section showing ascocarps of *L. conigenum* healthy and parasitised by *P. translucens* (× 25).
FIG. 60. Conidia and hyphae of *Cladosporium lophodermii* copied from the original illustration.
FIG. 61. Conidiophores of *C. lophodermii* copied from the original illustration.
FIG. 62. Ascocarp of *Lophodermium* showing pigmented hyphae possibly of *C. lophodermii*.

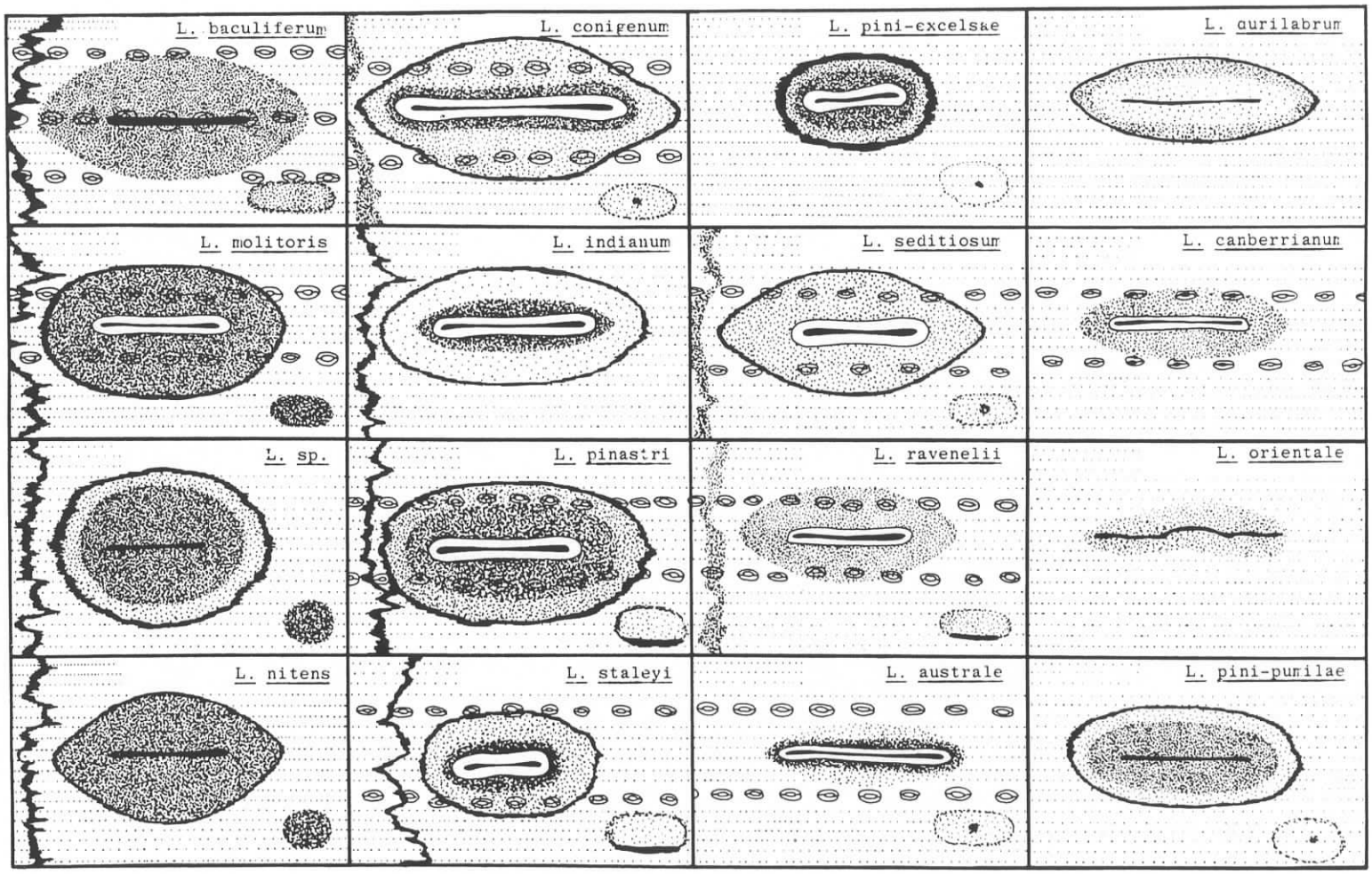


FIG. 63. Semi-diagramatic illustrations of each *Lophodermium* species.

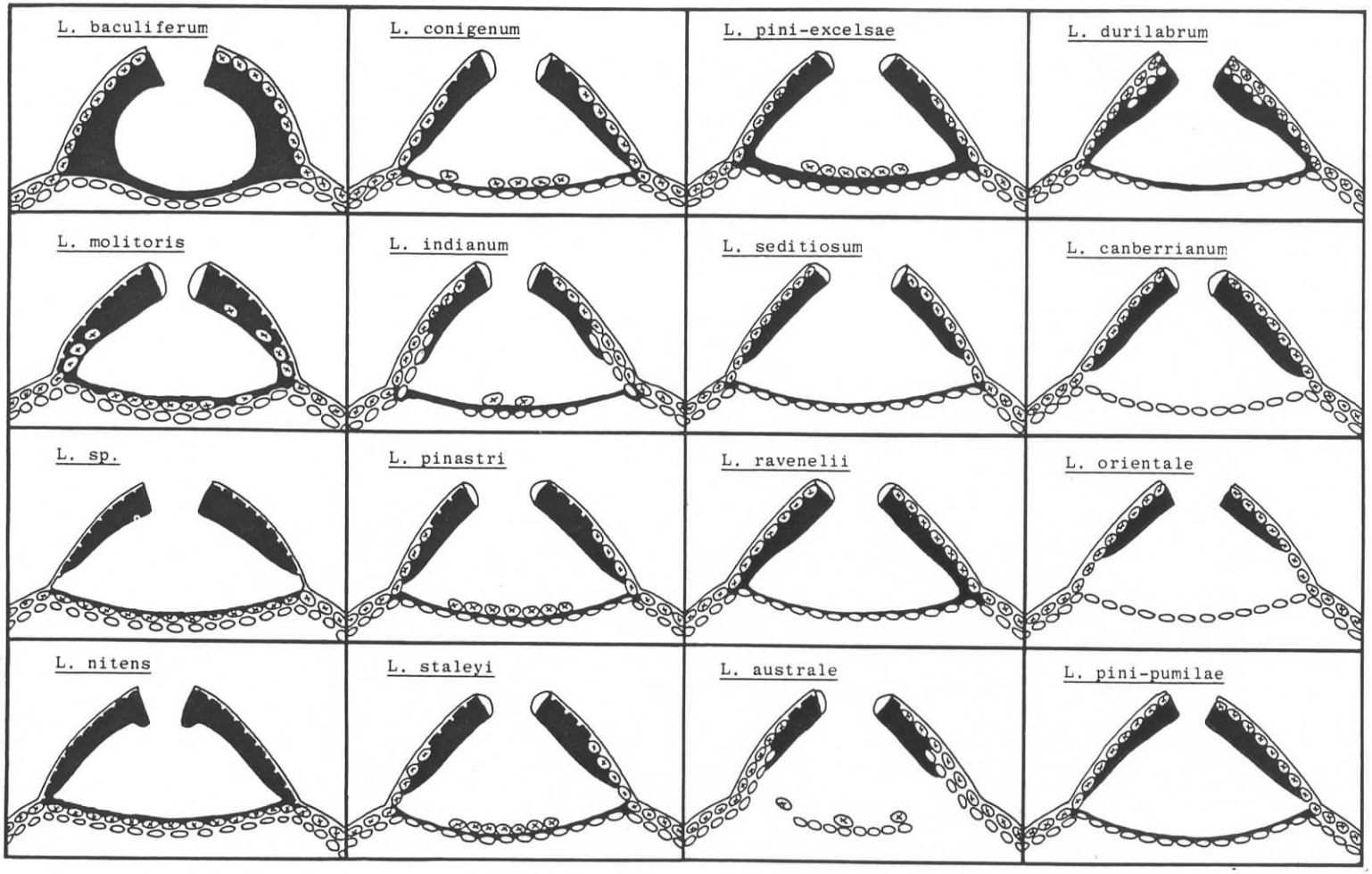


FIG. 64. Ascocarps in vertical section of each *Lophodermium* species illustrated diagramatically.

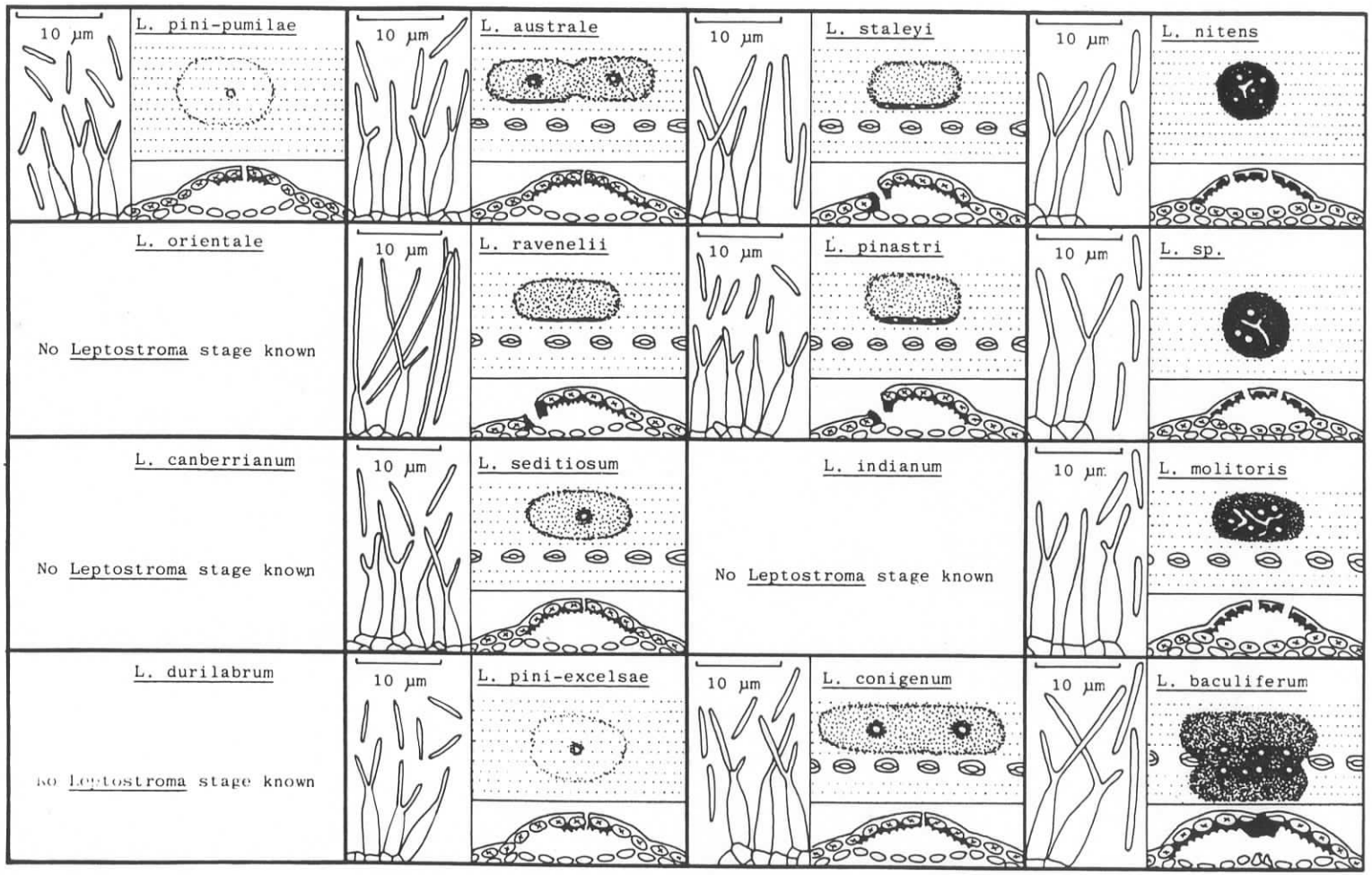


FIG. 65. Summary of the morphology of *Lophodermium* anamorphs.